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BULB FORMATION IN SOME AMERICAN AND EUROPEAN VARIETIES OF ONIONS AS AFFECTED BY LENGTH OF DAY [1]

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INTRODUCTION

Since the work of Garner and Allard (*3*) ,[2] presenting the specific effects of length of day upon plants, it has been recognized that bulbing of the onion (*Allium cepa* L.) is more or less dependent upon a suitable length of day, or photoperiod. Such work as has been done with the onion indicates that its flower and seed development is also favored by the longer days. In this respect it is a long-day type of plant, as the term has been used for those plants that produce their flower primordia in response to an increasing length of day. The onion is of especial interest, however, because its bulb, which represents a very compact and ball-like type of rosette, is best formed in response to long photoperiods. Many of the biennial or perennial long-day type of plants produce loose flat rosettes under the decreasing lengths of day of autumn.

Morphologically the onion bulb represents an intermediate stage of rosette development between the loose flat rosette of persistent green leaves and the extreme reduction of the rosette to mere scales as in the lily bulb. In the onion, green leaves are produced; but these ultimately die down, leaving only the swollen and thickened leaf bases alive and succulent. Thus, bulbing of the onion, which illustrates different phases of purely vegetative development, assumes especial interest because definite photoperiods give rise to particular phases of purely vegetative expression and to differences in the period of dormancy.

In the case of the hogpeanut, a wild legume, it has been shown by Allard (*1*) that the development of different types of flowers, including the initiation of the subterranean sort, is dependent upon particular lengths of day, so that in this plant different phases of flower development are governed by different photoperiods.

Difficulties of a practical nature also led the writers to make the present studies. Most of the varieties commonly grown in the late onion-growing sections of the United States fail to bulb normally when grown in southern Texas. Other varieties commonly grown in the Southern States have failed to produce satisfactory crops in the Northern States. On occasions when a shortage of onion seed existed

[1] Received for publication May 12, 1936; issued June 1937.
[2] Reference is made by number (italic) to Literature Cited, p. 751.

in this country, seed from northern European countries was imported, but the plants therefrom in many cases failed to produce normal, marketable bulbs. These failures have been attributed to many causes, chiefly seasonal. The present studies were initiated in an attempt to determine the role of length of day in the bulb formation of 18 varieties of onions commonly grown in the United States, 8 varieties commonly grown in northern European countries, and 2 varieties from other European countries.

REVIEW OF LITERATURE

Garner and Allard (*4*) planted sets of onions of the Silverskin variety, May 14, in the greenhouse and outside. Part of the greenhouse plants were illuminated with electric light from sunset to midnight of each day. The other part received only the normal daylight (maximum, 14.9 hours). Both greenhouse lots and the outside control produced good bulbs, but the bulbs and foliage of the greenhouse material were smaller than those in the control lot grown outside. When 13 hours of daylight were supplied, each set produced several shoots or divisions, each of which eventually produced a small but normal bulb. In the lot receiving only 10 hours of daylight, none of the plants produced any semblance of a bulb but split into two or more individuals, and the foliage remained green and erect for an indefinite period. With only 5 hours of light, the plants produced weak, pale-green shoots, but no bulbs, and soon died.

Bos (*2*) reports failure to secure bulbs of Silberzwiebel (silver onion) strains in the greenhouse during the winter in the Netherlands, when the normal day length was extended to 12 hours by the use of electric-bulb illumination. However, good bulbs were formed when the period of total illumination was extended to 14 to 15 hours daily. By using a light period of 16 to 17 hours he was able to obtain sufficient bulb formation in 3 months to distinguish the early-maturing strain from the late-maturing, the globe-shaped from the pear-shaped, the fine-textured from the coarse-textured, and the white mature skin color from the yellow and the red.

McClelland (*6*), working at Mayaguez, Puerto Rico, with four varieties of onions planted at different dates and grown under light exposures of 10, 11, 13.5, and 15 hours, respectively, and 11.0 to 13.2 hours (normal day), found that Prizetaker remained in the vegetative condition and produced slight or no swelling of the base in the 10- or 11-hour days. In the normal-day lot the response varied with the date of planting. In the lot planted November 14 and removed June 11, one of the five plants had developed a well-formed bulb 5.8 cm in diameter and the tops, though still green, had fallen over on removal at 30 weeks, whereas the others in the container were in the spring-onion stage, with erect turgid tops. In the lot planted December 12 and removed June 4, bulbs of considerable size had formed. Since with one exception the tops were still growing and were larger and more turgid than those under the shorter light exposure, the stage of development appeared to be intermediate between that of spring onions and matured bulbs. In the 13.5-hour lot, as in the other lots, the development was mainly that of spring onions although some plants were slightly swollen near the base.

Under a 15-hour day, the Prizetaker variety produced 100 percent of good bulbs in 30 weeks from the date of seed sowing. At 35 weeks the tops of 60 percent were dead and the other 40 percent were dying. McClelland says: "There was no evidence as to any effect of length of daily light exposure on division or splitting of the individual into more than one."

The Bermuda White variety, when grown under a 10-hour daily light exposure, remained in the spring-onion condition, a slightly swollen base being the nearest approach to bulb formation. McClelland says:

> Similarly, under an 11-hour daily light exposure the development for the most part was that of spring onions. Of those in the five plantings (total of 25 plants) only one individual developed bulbs.

Under normal-day exposures all plants developed normal bulbs, which at 25 to 30 weeks were entering or had entered the rest period. Well-formed bulbs developed under the 13.5-hour light exposure. On some of these the tops had fallen over at 20 weeks and were dead at 22 weeks. McClelland states:

> Under the 15-hour daily light exposure, bulbs developed rapidly though they were somewhat smaller. At 18 weeks the tops of these small well-formed bulbs had fallen over but were still green. At 20 weeks the tops were dead or dying.

The production of splits and doubles was very pronounced in the Bermuda White variety. McClelland says:

> Owing to the vigorous top growth and the absence of bulb formation the splitting of one individual into several was more conspicuous under the shorter exposures than under the longer daily light exposures where bulbs were quickly formed and the rest period was entered. On resumption of growth however, the compound formation under the longer exposures became evident.

Yellow Globe Danvers plants produced no good bulbs in the 10- and 11-hour lots. In the 13.5-hour and normal-day lots, planted on September 19 and not harvested until September 4 of the following year, small bulbs averaging 4.3 cm in diameter were formed. The tops had fallen over at 50 weeks and were dead at 51 weeks. Under the 15-hour exposure all had formed, or were forming, bulbs at 25 weeks from planting and the tops of all were dead at 31 weeks. Only 3 out of 81 plants of this variety showed splitting, 1 in the 11-hour, 1 in the normal-day, and 1 in the 15-hour lots.

Silver King (Giant White Tripoli) plants produced no good bulbs in the 10- or 11-hour lots. Development was not uniform in the normal-day lot or in the 13.5-hour lot, both lots producing various degrees of bulbing. The 13.5-hour lot, however, produced a greater percentage of bulbs that ripened normally, and the proportion of green-top plants with swollen bases was higher than in the normal-day lot. Under the 15-hour exposure all the plants formed bulbs.

Wilson (*8*), working with plants grown in water cultures from sets of the Yellow Strasburg variety, found that plants grown from March 19 to May 2 at Ithaca, N. Y., in a greenhouse that was maintained at a temperature of 60° to 70° F., produced only faint traces of bulbing. The length of possible daylight during this period varied from 12.2 to 14.2 hours. When plants of the same variety were grown from June 12 to July 15 in the greenhouse, where temperatures frequently reached 90°, all produced good bulbs. During this period the day length varied from an initial of 15.25 hours to a maximum of 15.3 hours, decreasing after the summer solstice to 14.9 hours.

In a third experiment, plants of the Ebenezer variety were grown from January 4 to February 27 in a greenhouse maintained at a temperature of 55° to 60° F. for the first 3 weeks and at 60° to 70° thereafter. Artificial light was supplied by 100-watt Mazda lamps suspended 3 feet above the cultures from dark until 10 o'clock each night. This resulted in an illumination period, including daylight and artificial light, of from 14.3 to 15.3 hours. Wilson says that under these conditions "many of the plants in this experiment failed to form distinct bulbs." Regarding bulbing he concludes (*8, p. 54*):

> Bulbing was related first of all to the length of day, secondly to the amount of root injury, and finally to the general vigor of the plant. Bulbing was first evident at pH 3.5, at pH 4.0, and in distilled water. Within a given reaction series, bulbing occurred first on the least thrifty plants. However, from the standpoint of total dry weight at the end of the experiment, the largest bulbs were found on the most vigorous plants, particularly in experiment 2, where bulbing was most pronounced.

In a recent paper Wilson (*9*) concludes that "apparently, initial bulbing results from the accumulation of sugars in all parts of the plants." He also found that "for some reason, large quantities of soil nitrates tend to delay bulb formation and to reduce yields." Nitrogen starvation, on the other hand, is characterized by a stunted growth, pale-green or even yellowish leaves, a rigidly erect position of the leaves, and a failure of the roots to die at the same time as those of normal plants. Small, distinct, bulbs were formed, but the necks neither collapsed nor ripened as in normal maturity. Soil moisture was found to limit the total amount of growth but apparently did not influence the time of bulbing.

1934 EXPERIMENT

MATERIALS

The 18 varieties used in 1934 included representatives of all the major types of onions grown in the United States. Yellow Bermuda, largely grown in Texas, is an early-maturing variety with light-yellow skin and mild-flavored flesh. White Creole is an early-maturing variety with hard, pungent flesh and is grown almost exclusively in Louisiana and adjoining States. Early Grano, recently improved and introduced by the New Mexico Agricultural Experiment Station, is an early variety of Spanish origin, with a light-yellow skin and mild flesh. Early Yellow Globe and Mountain Danvers are second-early varieties with hard, pungent flesh. California Early Red, recently developed at the California Agricultural Experiment Station, is an early, semiflat variety with soft, mild flesh. A strain of Australian Brown, also developed at the California Agricultural Experiment Station, is late maturing and has very firm, pungent flesh. Italian Red, likewise developed by the California Agricultural Experiment Station, is a midseason variety. It is long oval or bottle-shaped, with soft, mild-flavored flesh. Sweet Spanish (Utah Agricultural College strain) is a late-maturing sort, globe-shaped, with mild flesh, and is grown extensively in Washington, Oregon, Utah, Colorado, and California. This variety can be grown successfully in all parts of the United States by starting the seedlings in greenhouses. The remaining varieties, including Yellow Strasburg, Ebenezer, Ohio Yellow Globe, Yellow Danvers Flat, Yellow Globe Danvers, White Portugal, Red Wethersfield, Southport Red Globe, and Southport Yellow

Globe, are all midseason to late maturing, with hard, pungent flesh characteristic of the varieties grown for storage in the Northern States.

With the exception of the Ebenezer variety, which came from the California Agricultural Experiment Station, all the midseason to late varieties were obtained from commercial sources. They were the most uniform strains submitted for use in the vegetable variety standardization project of the Bureau of Plant Industry, United States Department of Agriculture, and cooperating State experiment stations.

METHODS

Seed was sown in the greenhouse at the Arlington Experiment Farm, Arlington, Va., near Washington, D. C., December 20, 1933, and the plants grew slowly at a cool temperature until March 26, 1934, when they were transplanted into the experimental boxes. At this time they were approximately 8 to 9 inches tall and one-eighth to three-sixteenths of an inch in diameter at a distance of one-half inch above the root plate. All but 6 inches of the tops and 1½ inches of the roots were removed preparatory to planting. The trimmed plants were spaced 2 inches apart in rows 4 inches apart, in boxes 10 inches wide, 10 inches deep, and 36 inches long, inside measurements. Since limited space permitted the planting of only 10 plants of each variety in each treatment, 5 were planted in each of 2 boxes, which were placed on movable trucks. The duplicate boxes were separated from each other on the trucks in order to avoid restricting to certain varieties any possible favorable or unfavorable place effect.

A rich compost soil, to which had been added a liberal application of a commercial fertilizer containing 5 percent of nitrogen, 8 percent of phosphoric acid, and 5 percent of potash was used in the lower 8½ inches of each box. On top of the compost 1 inch of muck was placed in order to provide a substratum that would allow easy access to the base of the growing plant for examination of the amount of bulbing. Additional applications of the fertilizer mentioned and top dressings of nitrate of soda were made at weekly intervals until the bulbs were more than half grown; at no time was there any evidence of malnutrition.

Thrips were controlled by weekly sprays, and the plants made excellent growth. A rot that started at the base of the plants caused the loss of a few individuals after they had made their maximum vegetative growth.

The boxes of plants, except those of the control lot, were placed on movable trucks and were exposed to daylight according to the schedule given below. For the remainder of each day, the trucks containing the plants were kept in dark, ventilated houses.

10-hour day, 6 a. m. to 4 p. m.
12-hour day, 6 a. m. to 6 p. m.
13-hour day, 5 a. m. to 6 p. m.
13.5-hour day, 5 a. m. to 6.30 p. m.
14-hour day, 5 a. m. to 7 p. m.
14.25-hour day, 5 a. m. to 7.15 p. m.

Throughout the duration of the experiment the control plants remained outside, where they were exposed to the natural length of day, which at Washington, D. C., varied from 12.4 to a maximum of 14.9 hours for the period covered.

The 12-, 13-, 13.5-, 14-, and 14.25-hour lots also remained outside, exposed to the normal length of day, until the date when the possible hours of daylight from sunrise to sunset had reached the respective photoperiod for each treatment. These dates were as follows: 12-hour day, March 29; 13-hour day, April 10; 13.5-hour day, April 23; 14-hour day, May 6; 14.25-hour day, May 21.

To aid in interpreting the data, air temperatures as recorded on official United States Weather Bureau instruments in regulation instrument shelters are presented in table 1. The average temperature is the average of the minimum and maximum readings. The minimum temperature for the week ended March 31 occurred on the 25th, the day before the plants were set. The plants were well hardened before transplanting and none was killed by temperatures of 29°, 29°, and 28° F. on the successive dates of March 28, 29, and 30, respectively.

TABLE 1.—*Weekly average air temperatures and minimum and maximum for each week, at Arlington Experiment Farm, for seasons of 1934 and 1935*

Week ended—	Mar. 25 to Aug. 11, 1934					Week ended—	May 1 to Sept. 6, 1935				
	Mean (average)			Minimum	Maximum		Mean (average)			Minimum	Maximum
	Minimum	Maximum	Average				Minimum	Maximum	Average		
	°F.	°F.	°F.	°F.	°F.		°F.	°F.	°F.	°F.	°F.
Mar. 31	31	52	42	22	63	May 4	51	70	61	42	84
Apr. 7	43	68	56	35	82	May 11	50	72	61	46	82
Apr. 14	40	60	50	30	76	May 18	52	71	62	46	78
Apr. 21	45	65	55	34	72	May 25	50	69	60	44	72
Apr. 28	42	60	51	30	79	June 1	58	83	71	46	89
May 5	48	73	60	32	89	June 8	62	80	71	56	84
May 12	54	80	67	42	90	June 15	62	83	73	56	91
May 19	54	78	66	44	89	June 22	67	87	77	61	95
May 26	55	78	67	46	94	June 29	62	88	75	58	97
June 2	58	79	69	53	88	July 6	69	90	80	61	93
June 9	64	82	73	58	89	July 13	72	91	82	70	97
June 16	63	86	75	60	90	July 20	70	93	82	68	99
June 23	68	87	77	65	95	July 27	73	91	82	63	97
June 30	70	95	83	63	102	Aug. 3	70	92	81	60	98
July 7	71	94	83	68	96	Aug. 10	69	86	78	62	94
July 14	68	88	78	59	93	Aug. 17	72	96	84	68	101
July 21	69	96	83	61	99	Aug. 24	69	87	78	62	94
July 28	73	96	84	71	99	Aug. 31	61	82	72	55	88
Aug. 4	69	88	79	67	92	Sept. 6	63	72	68	55	76
Aug. 11	67	88	77	58	93						

Thermographs installed in the darkened sheds in earlier experiments revealed only slight differences (2° to 3° F.) between the temperature within the sheds and that outside, showing a somewhat higher temperature in the sheds, especially at night.

RESULTS

An excellent stand of plants was obtained in 1934, and growth proceeded at a rapid and apparently uniform rate under all treatments for the first 6 to 8 weeks after planting. By June 21 the plants in the lots receiving 10 and 12 hours of light were much taller and the blades were more erect than in the lots exposed longer. There was apparently a gradual reduction in height of plant from the 12- to the 14-hour treatments. However, measurements from

the soil surface to the tip of the longest leaf and of the diameter of the plant 2 inches above the soil level showed no significant difference in size between the different lots in any of the varieties. The apparent difference in size was due to the fact that the blades had broken over more in the long-day treatments than in the short-day treatments. The plants in the 10- and 12-hour lots, where bulbs did not form, continued to produce new leaves, which grew erect and remained so until they attained sufficient height to be beaten over by the wind and rain.

As the onion plant matures, the older leaves die and dry up, and the softening of the tissues in the column of leaf bases (neck) above the bulb finally allows the foliage, or top, to fall over. This dropping of the tops is recognized by commercial growers as an indication of maturity.

The length of day had a marked effect on the amount and rate of dropping of the tops. As early as May 15 the necks of some of the White Creole plants in the longer day treatments were beginning to soften and bend over. The condition of all the varieties on July 7 is shown in table 2. It was evident that, in general, increasing the length of day increased the percentage of plants whose tops had fallen over and also the percentage of plants with dry tops. Since the three categories of condition are successive stages in maturity, the increase in length of day appears to hasten maturity.

It is also apparent that there are at least four groups of varieties with reference to their maturity: Group 1 includes White Creole, Early Grano, and Yellow Bermuda; group 2, Ebenezer, Mountain Danvers, Yellow Strasburg, Early Yellow Globe, Ohio Yellow Globe, Yellow Danvers Flat, and Australian Brown; group 3, Red Wethersfield, White Portugal, Yellow Globe Danvers, Southport Red Globe. Southport Yellow Globe, California Early Red, and Italian Red; and group 4, Sweet Spanish (S1).

On July 7 none of the tops on any of the varieties tested had fallen over in the 10-hour treatment. Twelve hours of daylight was sufficient to initiate maturity in group 1, and 13 hours was sufficient for group 2. In group 3, 14 hours' exposure was required to cause the tops to drop; none of the Sweet Spanish plants (group 4) in any of the lots had the tops down on July 7.

When the time factor is considered, the difference in reaction between the 13.5- and 14-hour day in the varieties in group 3 is remarkable. An increase of less than 3.5 percent in the total duration of daylight over a period of 75 days was sufficient to cause the difference shown. Or, put in another way, a total difference of less than 35 hours, accumulated over a period of 75 days, resulted in the marked difference indicated in table 2.

The importance of the time element is seen by comparing the data in table 2 with those in table 4 (p. 729). On July 7 none of the tops of the Sweet Spanish plants had fallen over in any of the treatments, but by August 13 most of the tops were dry on plants in the 14-hour, 14.25-hour, and normal-day lots. Likewise the varieties in group 3, which on July 7 had none of the tops fallen over in the 13.5-hour treatment except two Italian Red plants, had all of them fallen over and most of them dry by August 13.

TABLE 2.—*Condition of foliage on July 7, 1934, in 18 varieties of onions exposed to different lengths of day*

Variety	Condition of foliage after daily exposure to indicated number of hours of daylight																				
	10			12			13			13.5			14			14.25			12.4–14.9		
	Erect and green [1]	Prostrate		Erect and green [1]	Prostrate		Erect and green [1]	Prostrate		Erect and green [1]	Prostrate		Erect and green [1]	Prostrate		Erect and green [1]	Prostrate		Erect and green [1]	Prostrate	
		Green [2]	Dry [3]		Green [2]	Dry [3]		Green [2]	Dry [3]		Green [2]	Dry [3]		Green [2]	Dry [3]		Green [2]	Dry [3]		Green [2]	Dry [3]
	Per-cent	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*
White Creole	100	0	0	25	63	12	0	60	40	0	50	50	0	0	100	0	0	100	0	0	100
Early Grano	100	0	0	70	30	0	30	60	10	0	50	50	0	60	40	0	33	67	0	30	70
Yellow Bermuda	100	0	0	50	50	0	50	50	0	20	60	20	0	100	0	0	80	20	0	80	20
Ebenezer	100	0	0	100	0	0	89	11	0	10	90	0	10	90	0	0	90	10	0	90	10
Mountain Danvers	100	0	0	100	0	0	60	40	0	22	78	0	10	90	0	0	100	0	0	90	10
Yellow Strasburg	100	0	0	100	0	0	67	33	0	80	20	0	0	100	0	0	90	10	0	100	0
Early Yellow Globe	100	0	0	100	0	0	80	20	0	70	30	0	20	80	0	0	100	0	0	70	30
Ohio Yellow Globe	100	0	0	100	0	0	80	20	0	60	40	0	0	78	22	0	80	20	0	100	0
Yellow Danvers Flat	100	0	0	100	0	0	100	0	0	60	40	0	30	70	0	0	100	0	10	90	0
Australian Brown	100	0	0	100	0	0	89	11	0	70	30	0	40	40	20	0	80	20	40	60	0
Red Wethersfield	100	0	0	100	0	0	100	0	0	100	0	0	0	100	0	0	100	0	10	90	0
White Portugal	100	0	0	100	0	0	100	0	0	100	0	0	20	80	0	10	90	0	0	100	0
Yellow Globe Danvers	100	0	0	100	0	0	100	0	0	100	0	0	0	100	0	30	70	0	10	90	0
Southport Red Globe	100	0	0	100	0	0	100	0	0	100	0	0	30	70	0	50	50	0	10	90	0
Southport Yellow Globe	100	0	0	100	0	0	100	0	0	100	0	0	50	50	0	20	40	40	50	50	0
California Early Red	100	0	0	100	0	0	100	0	0	100	0	0	50	50	0	30	70	0	20	80	0
Italian Red	100	0	0	100	0	0	100	0	0	80	20	0	50	50	0	44	55	0	22	78	0
Sweet Spanish (81) [4]	100	0	0	100	0	0	100	0	0	100	0	0	100	0	0	100	0	0	100	0	0

[1] Petiole column turgid and majority of leaves green and succulent.
[2] Petiole column flaccid and bent over and majority of leaves green and succulent.
[3] Petiole column flaccid and bent over and all the leaves dry.
[4] S followed by a number indicates a separate strain.

The same general grouping of varieties for earliness of maturity (based on drying of the tops) holds for the data collected on August 13 (table 4) as for that of July 7 (table 2), although the order is somewhat different within each group. California Early Red was in group 3 on July 7 and in group 2 on August 13.

The condition of the foliage on July 17, 1934, is shown in figure 1. The effect of increasing the length of day on the rate of maturity was clearly shown by the greater degree of desiccation and the greater percentage of plants whose tops had fallen over as the length of day increased from 10 hours to 14.9 hours (fig. 1, *G*). Yellow Bermuda (*a*), White Creole (*d*), Early Yellow Globe (*c*), and Early Grano (*h*) were the only varieties maturing in the 12-hour day treatment and were the most mature in all the treatments. Sweet Spanish (*f*) and Italian Red (*g*) required the longest daily light exposure or exposure over the greatest number of days. The single plant of Sweet Spanish (*f*) with erect foliage in the control (normal-day) treatment, is illustrative of the unevenness of foliage dropping which is characteristic of this variety.

Because of the closeness of planting it was impossible to make accurate measurements of bulb development without seriously injuring the foliage, so rating was resorted to in recording the relative development of the bulb.

The first reading was made on July 7 and the terms none, slight, fair, medium, and good were used to describe the development of the base of the plant. The results are given in table 3 in the approximate order of bulb development. The percentage of each type of bulb was used in deciding the order but was omitted from the table for brevity.

TABLE 3.—*Degree* [1] *of bulb formation on July 7, 1934, in 18 varieties of onions exposed to different lengths of day*

Variety	Bulb formation after daily exposure to indicated number of hours of possible sunlight						
	10	12	13	13.5	14	14.25	12.4–14.9
Yellow Bermuda	0–sl.	g.	g.	g.	g.	g.	g.
White Creole	0	g.	g.	g.	g.	g.	g.
Early Grano	0–sl.	sl.–g.	g.	g.	g.	g.	g.
Early Yellow Globe	0	0–f.	sl.–g.	g.	g.	g.	g.
Mountain Danvers	0	0	f.–g.	f.–g.	g.	g.	g.
California Early Red	0	0	sl.–f.	f.–g.	g.	g.	g.
Yellow Strasburg	0	0	sl.–m.	f.–m.	f.–g.	g.	g.
Ebenezer	0	0	f.–m.	f.–m.	f.–g.	g.	g.
Ohio Yellow Globe	0	0	sl.–m.	f.–m.	f.–g.	g.	g.
Yellow Danvers Flat	0	0	sl.–m.	f.–m.	f.–g.	g.	g.
Australian Brown	0	0	sl.–f.	f.–m.	f.–g.	g.	g.
Yellow Globe Danvers	0	0	sl.–f.	f.–m.	f.–g.	f.–g.	g.
White Portugal	0	0	sl.–f.	sl.–f.	f.–g.	g.	g.
Red Wethersfield	0	0	0–sl.	f.–m.	f.–g.	g.	g.
Southport Red Globe	0	0	sl.–f.	sl.–f.	f.–g.	f.–g.	g.
Southport Yellow Globe	0	0	0–sl.	sl.–f.	f.–g.	f.–g.	f.–g.
Italian Red	0	0	0–f.	sl.–m.	f.–m.	f.–m.	f.–g.
Sweet Spanish (S1) [2]	0	0	0–sl.	sl.–f.	sl.–f.	sl.–f.	f.–m.

[1] Degrees of bulb formation: 0, none; sl., slight; f., fair; m., medium; g., good.
[2] S followed by a number indicates a separate strain.

Yellow Bermuda and Early Grano were the only varieties to produce any swelling of the base in the 10-hour treatment, and the percentages of plants in the "slight" class were only 20 and 10, respectively. In the 12-hour treatment White Creole, Yellow Bermuda, and Early

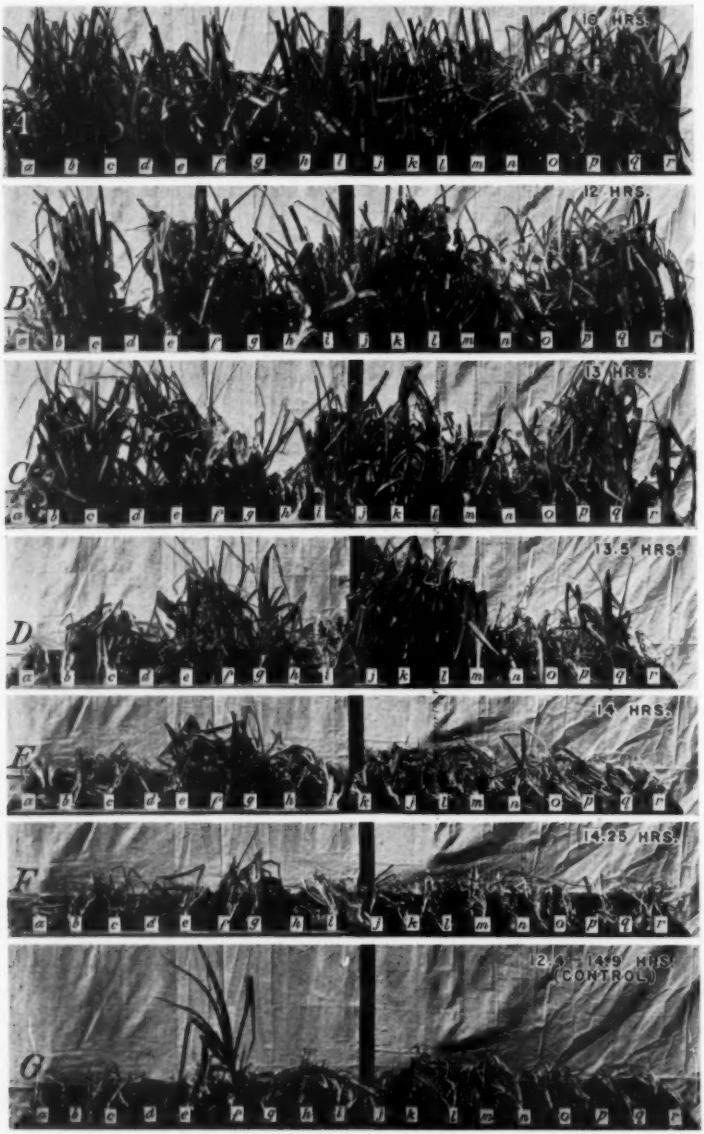

FIGURE 1.—Condition of foliage July 17, 1934, in 18 varieties of onions grown at Arlington Experiment Farm under different daily periods of normal daylight as indicated: *A*, 10 hours; *B*, 12 hours; *C*, 13 hours; *D*, 13.5 hours; *E*, 14 hours; *F*, 14.25 hours; *G* (control), normal day length (12.4 to 14.9 hours). Ruler in background marked in inches. Letters in front of rows refer to following varieties: *a*, Yellow Bermuda;

Grano were the only varieties to produce good bulbs. Early Yellow Globe produced one bulb that was rated as fair in the 12-hour lot. At the other end of the scale is Sweet Spanish, which had produced no well-bulbed plants by July 7 in even the longest days. This, however, is a late-maturing variety and had not had sufficient time to make bulbs.

In order to save the bulbs of the early-maturing varieties from rotting it was necessary to terminate the experiment on August 13. Notes were made on the condition of the foliage and the amount of bulb formation on all plants available. A representative sample of the plants of every variety was photographed and varieties typical of the different groups are shown in figures 2 to 5. To save space on the photographs, most of the leaf blades were removed from plants on which the neck was still green and succulent, and all of the foliage above the neck was removed when the neck was dry.

The foliage was recorded as green when more than one blade retained its green color and the neck retained some noticeable moisture. The foliage of plants of this type was removed before the plants were photographed, but where the neck was stiff and succulent, though fallen over, the basal portion of the blades and the neck were allowed to remain.

Data on bulbs and foliage are recorded in table 4. All the plants that had dry tops on August 13 had good bulbs. Size was not considered in rating the bulbs, but only the degree to which the base of the plant had swollen.

Yellow Bermuda was the only variety to produce a good bulb that eventually dried down normally in the 10-hour day. Early Grano, White Creole, and Yellow Bermuda made 100 percent of good bulbs in the 12-hour day. Early Yellow Globe produced 22 percent and White Portugal 11 percent of well-bulbed plants. None of the other varieties produced any good bulbs in the 12-hour day. All of the varieties except Sweet Spanish produced some good bulbs with dry tops in the 13-hour day, and none of the varieties produced any plants that rated below medium-bulbed. Therefore 13 hours of daylight proved sufficient to produce bulbs on all of the varieties studied.

Exposures longer than 13 hours hastened the maturity of the bulb. With regard to rate of maturity there are four groups. The first group comprises Yellow Bermuda, Early Grano, and White Creole; the second, California Early Red, Early Yellow Globe, Yellow Strasburg, Ebenezer, Mountain Danvers, Ohio Yellow Globe, Yellow Danvers Flat, and Australian Brown; the third, Yellow Globe Danvers, White Portugal, Red Wethersfield, Southport Red Globe, Southport Yellow Globe, and Italian Red; and the fourth, Sweet Spanish.

FIGURE 1.—Continued.
b, California Early Red; *c*, Early Yellow Globe; *d*, White Creole; *e*, Southport Yellow Globe; *f*, Sweet Spanish; *g*, Italian Red; *h*, Early Grano; *i*, White Portugal; *j*, Yellow Globe Danvers; *k*, Red Wethersfield; *l*, Yellow Strasburg; *m*, Australian Brown; *n*, Yellow Danvers Flat; *o*, Ohio Yellow Globe; *p*, Ebenezer; *q*, Southport Red Globe; *r*, Mountain Danvers. Note the erect succulent foliage and necks of all varieties in the 10-hour lot (*A*) and of most of the varieties in the 12-hour lot (*B*), and the effect of increasing day length on the dropping and dying of the foliage. Yellow Bermuda (*a*), White Creole (*d*), and Early Grano (*h*) are the only varieties with dying foliage in the 12-hour treatment (*B*). The single erect plant of Sweet Spanish (*f*) in the control lot is illustrative of the variability in foliage drop which is characteristic of this variety in the field. This plant finally produced a normal bulb. The later maturity of this variety and of Southport Yellow Globe (*e*) and Italian Red (*q*) is shown by their greener condition under the longer lengths of day.

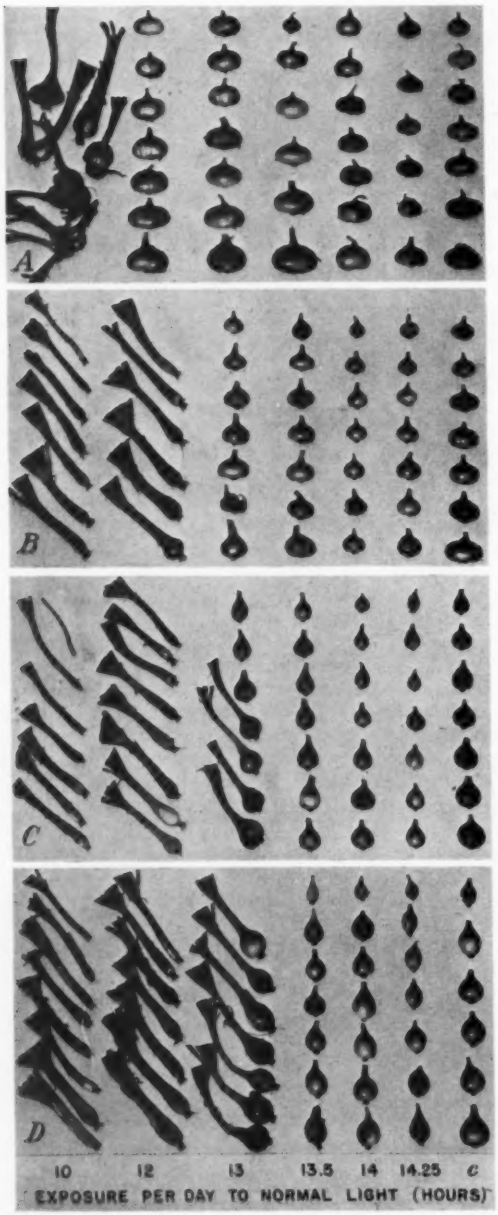

FIGURE 2.—Degree of bulbing and condition of neck and foliage on August 13, 1934, in a representative sample of onion varieties: *A*, Yellow Bermuda; *B*, Yellow Strasburg; *C*, Australian Brown; and *D*, Southport Yellow Globe. Control (*c*) grown under normal length of day (12.4–14.9 hours). No foliage on bulb indicates that foliage was dead or nearly so. The right-hand double in 10-hour treatment of Yellow Bermuda (*A*) was the only plant in any variety that matured a good or normal bulb at this exposure. In the 13-hour lot, 22 percent of Australian Brown (*C*) and 40 percent of Southport Yellow Globe (*D*) were bottlenecks when dried.

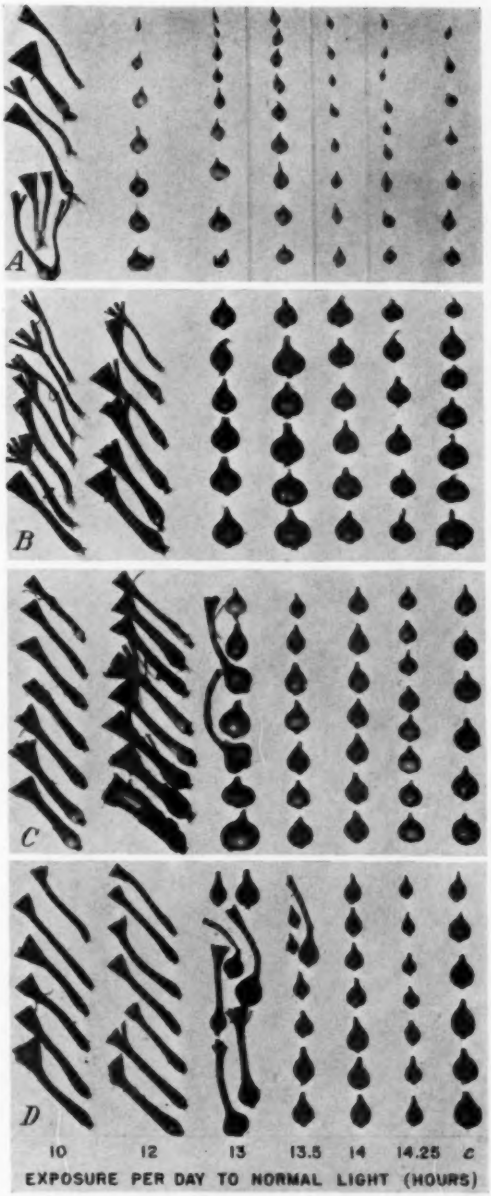

FIGURE 3.—Degree of bulbing and condition of neck and foliage on August 13, 1934, in a representative sample of onion varieties: *A*, White Creole; *B*, California Early Red; *C*, Mountain Danvers; and *D*, Southport Red Globe. Control (c) grown under normal length of day (12.4–14.9 hours). No foliage on bulb indicates that foliage was dead or nearly so. These varieties are arranged (from top to bottom) in order of earliness of maturity.

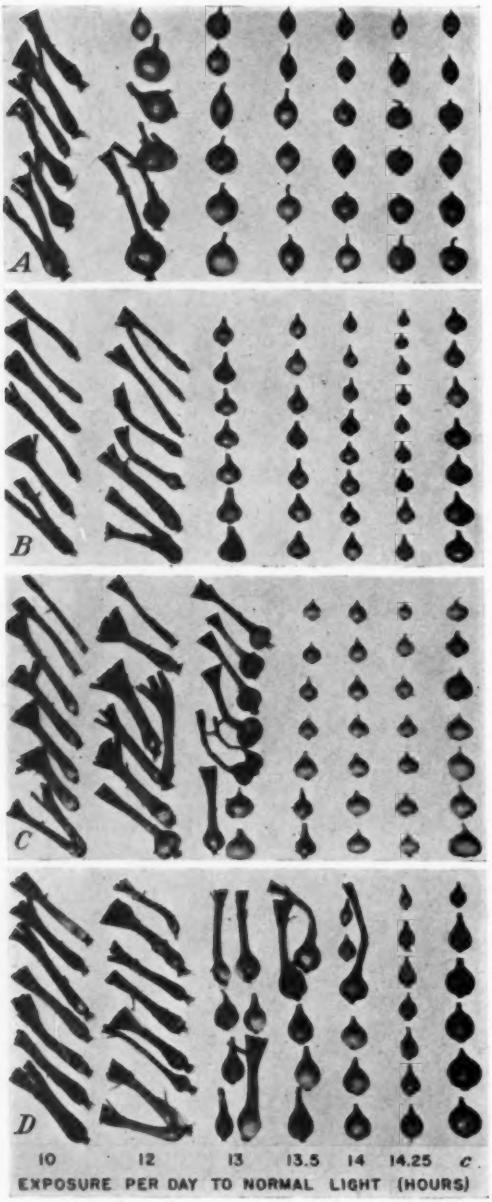

FIGURE 4.—Degree of bulbing and condition of neck and foliage on August 13, 1934, in a representative sample of onion varieties: *A*, Early Grano; *B*, Ebenezer; *C*, White Portugal; and *D*, Yellow Globe Danvers. Control (*c*) grown under normal length of day (12.4–14.9 hours). No foliage on bulb indicates that foliage was dead or nearly so. Note the slight swelling of the base of some of the Early Grano (*A*) plants in the 10-hour lot and the variability in maturity which existed in the White Portugal (*C*) and Yellow Globe Danvers (*D*) varieties. All of the plants with green foliage in the Yellow Globe Danvers variety failed to produce normal bulbs.

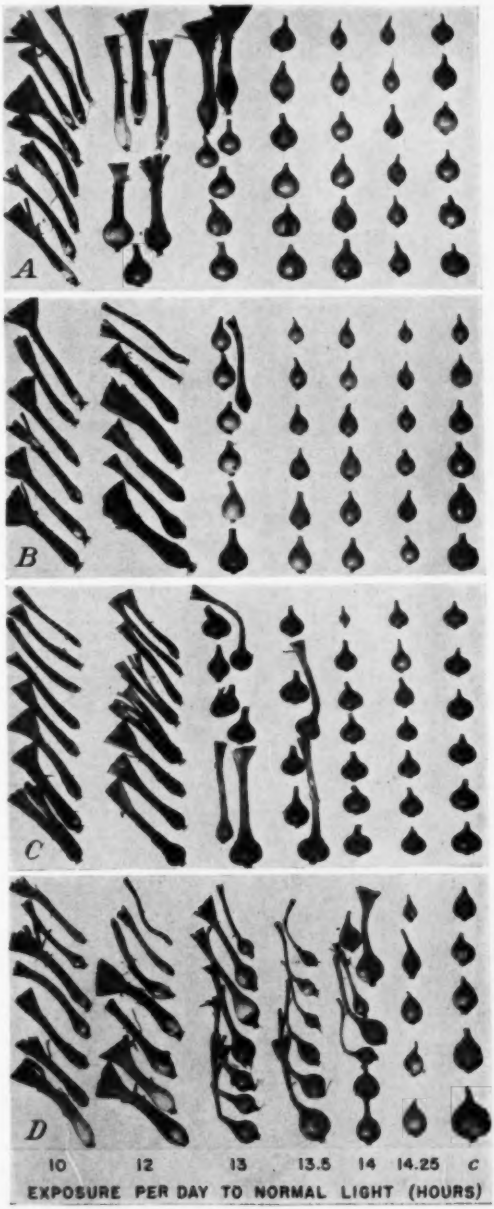

FIGURE 5.—Degree of bulbing and condition of neck and foliage on August 13, 1934, in a representative sample of onion varieties: *A*, Early Yellow Globe; *B*, Ohio Yellow Globe; *C*, Red Wethersfield; and *D*, Sweet Spanish. Control (*c*) grown under normal length of day (12.4–14.9 hours). No foliage on bulb indicates that foliage was dead or nearly so. Note the one good bulb in the 12-hour lot of Early Yellow Globe (*A*) and the two scallions in the 13-hour lot. The single plant of Ohio Yellow Globe (*B*) that failed to produce a good bulb in the 13-hour treatment is shown. The smallest plant in the 13-hour lot of Red Wethersfield (*C*) represents the scallion. The other two with foliage dried down to bottlenecks, as did the two with foliage in the 13.5-hour lot. All of the plants in the 13.5- and 14-hour lots of Sweet Spanish (*D*) ripened down into good bulbs, while of those in the 13-hour lot, 11 percent were bottlenecks and 22 percent stiff necks.

TABLE 4.—*Condition of foliage and degree of bulb formation on August 13, 1934, in 18 varieties of onions exposed to different lengths of day*

Variety	Condition of plants after daily exposure to indicated number of hours of daylight																			
	10				12					13			13.5		14		14.25		12.4–14.9	
	Green foliage, base showing indicated degree of swelling				Green foliage, base showing indicated degree of swelling				Dry foliage, good bulbs	Green foliage, base showing indicated degree of swelling		Dry foliage, good bulbs	Green foliage, good bulbs	Dry foliage, good bulbs	Green foliage, good bulbs	Dry foliage, good bulbs	Green foliage, good bulbs	Dry foliage, good bulbs	Dry foliage, good bulbs	
	None	Slight	Medium	Much	None	Slight	Medium	Much		Medium	Much									
	Pct.	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	
Yellow Bermuda	0	11	67	22	0	0	0	0	100	0	0	100	0	100	0	100	0	100	100	
Early Grano	0	33	67	0	0	0	0	22	78	0	0	100	0	100	0	100	0	100	100	
White Creole	50	17	33	0	0	0	0	0	100	0	0	100	0	100	0	100	0	100	100	
California Early Red	100	0	0	0	0	100	0	0	0	0	0	100	0	100	0	100	0	100	100	
Early Yellow Globe	63	37	0	0	0	57	22	11	11	20	0	80	0	100	0	100	0	100	100	
Yellow Strasburg	100	0	0	0	43	43	14	0	0	0	0	100	0	100	0	100	0	100	100	
Ebenezer	89	11	0	0	56	44	0	0	0	0	0	100	0	100	0	100	0	100	100	
Mountain Danvers	29	57	14	0	10	90	0	0	0	0	20	80	0	100	0	100	0	100	100	
Ohio Yellow Globe	100	0	0	0	60	30	10	0	0	11	11	78	0	100	0	100	0	100	100	
Yellow Danvers Flat	100	0	0	0	100	0	0	0	0	0	11	89	0	100	0	100	0	100	100	
Australian Brown	100	0	0	0	56	44	0	0	0	0	44	56	0	100	0	100	0	100	100	
Yellow Globe Danvers	100	0	0	0	30	50	20	0	0	30	10	60	56	44	10	90	0	100	100	
White Portugal	100	0	0	0	33	56	0	11	0	11	56	33	20	80	0	100	0	100	100	
Red Wethersfield	100	0	0	0	20	70	10	0	0	20	20	60	50	50	0	100	0	100	100	
Southport Red Globe	100	0	0	0	90	10	0	0	0	33	56	11	14	86	0	100	0	100	100	
Southport Yellow Globe	100	0	0	0	70	30	0	0	0	0	80	20	75	25	10	10	0	100	100	
Italian Red	100	0	0	0	50	50	0	0	0	0	63	37	33	67	12	88	0	100	100	
Sweet Spanish (S1) [1]	60	40	0	0	10	90	0	0	0	0	100	0	100	0	22	78	20	80	100	

[1] S followed by a number indicates a separate strain.

Onions that fail to mature at the same time as the majority of the crop usually produce only bottlenecks or scallions if left longer in the field. Scallions may be defined as onions with thick necks and relatively small and poorly developed bulbs; bottlenecks, as onions with abnormally thick necks. Neither type is accepted in the U. S. No. 1 grade of onions nor is considered a good bulb.

In order to determine the number of good bulbs among plants having green foliage and succulent necks on August 13, the plants were dried for about 2 months and then classified as good bulbs, scallions, and bottlenecks. The percentages of scallions and bottlenecks are given in table 5 and show that Yellow Bermuda was the only variety to produce good bulbs with a 10-hour day. Yellow Bermuda, Early Grano, and White Creole produced 100 percent of good bulbs in the lots exposed 12 hours or longer. In addition to the three varieties just mentioned, Early Yellow Globe was the only variety to mature good bulbs in the 12-hour lot. The bulbs of Early Yellow Globe and White Portugal, rated as having a much-swollen base with green foliage in the 12-hour lot in table 3, turned out to be bottlenecks. In the 13-hour lot, two-thirds of the medium-bulb plants with green foliage proved to be scallions when dried, but only 31 percent of the much-swollen plants proved to be bottlenecks when dried. In the 13.5-hour lot only 28 percent of the well-bulbed plants with green tops proved to be bottlenecks and they were not extreme types. In the 14-hour lot only 20 percent of the bulbs with green tops were found to be bottlenecks and none of them proved to be scallions when dried.

TABLE 5.—*Percentages of plants showing scallions and bottlenecks in onions exposed to different lengths of day in 1934*

Variety	Plants showing indicated formations under specified number of hours of daylight [1]							
	10		12		13		13.5	14
	Scallions	Bottlenecks	Scallions	Bottlenecks	Scallions	Bottlenecks	Bottlenecks	Bottlenecks
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Yellow Bermuda	40	50	0	0	0	0	0	0
Early Grano	100	0	0	0	0	0	0	0
White Creole	78	22	0	0	0	0	0	0
California Early Red	100	0	100	0	0	0	0	0
Early Yellow Globe	100	0	78	11	20	0	0	0
Yellow Strasburg	100	0	100	0	0	0	0	0
Ebenezer	100	0	100	0	0	0	0	0
Mountain Danvers	100	0	100	0	0	20	0	0
Ohio Yellow Globe	100	0	100	0	11	0	0	0
Yellow Danvers Flat	100	0	100	0	0	0	0	0
Australian Brown	100	0	100	0	0	22	0	0
Yellow Globe Danvers	100	0	100	0	22	11	33	10
White Portugal	100	0	89	11	11	22	0	0
Red Wethersfield	100	0	100	0	11	22	33	0
Southport Red Globe	100	0	100	0	11	22	14	0
Southport Yellow Globe	100	0	100	0	0	40	0	0
Italian Red	100	0	100	0	0	33	22	0
Sweet Spanish (S1) [2]	100	0	100	0	22	11	0	0

[1] No scallions were found in the 13.5-hour, 14.25-hour, nor in the 12.4- to 14.9-hour lots; no bottlenecks were found in the 14.25-hour nor in the 12.4- to 14.9-hour lots.

[2] S followed by a number indicates a separate strain.

Other types of onions that are objectionable from the commercial standpoint are "doubles" and "splits." Doubles are bulbs in which the outer scale has split, revealing two or more divisions joined at the base. Splits are bulbs in which the outer scale is intact but the bulb so misshapen as to indicate two or more divisions within. Plants of these types were recorded when the material was harvested on August 13. The combined results (doubles and splits), shown in table 6, indicate that, although doubling and splitting are largely varietal characteristics, minimal and subminimal lengths of day for bulbing tend to increase their prevalence.

TABLE 6.—*Percentage of plants showing doubles and splits in 18 varieties of onions exposed to different lengths of day in 1934*

Variety	Plants showing doubles and splits under specified number of hours of daylight						
	10	12	13	13.5	14	14.25	12.4–14.9
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Yellow Bermuda	70	20	0	0	0	13	10
Early Grano	42	22	0	0	0	0	0
White Creole	33	10	10	0	0	0	0
California Early Red	0	0	0	14	0	0	0
Ebenezer	33	22	10	0	0	0	10
Yellow Danvers Flat	30	20	11	0	0	0	10
Yellow Strasburg	0	0	12	25	0	0	12
Mountain Danvers	0	10	0	0	0	0	0
Early Yellow Globe	0	0	10	0	0	0	0
Ohio Yellow Globe	0	20	0	0	0	0	0
Australian Brown	0	0	0	0	0	0	0
White Portugal	20	33	0	0	0	0	0
Red Wethersfield	12	30	30	0	0	10	0
Southport Red Globe	0	0	0	0	0	0	0
Italian Red	0	0	12	0	0	0	0
Yellow Globe Danvers	10	10	0	0	0	0	0
Southport Yellow Globe	10	0	0	0	0	0	0
Sweet Spanish (S1) [1]	0	0	0	0	0	0	0

[1] S followed by a number indicates a separate strain.

Under the conditions of this experiment an exposure of 12 hours of daylight was sufficient for good bulb formation in the Yellow Bermuda, Early Grano, and White Creole varieties. California Early Red, Yellow Strasburg, Ebenezer, and Yellow Danvers Flat produced 100 percent of good bulbs when exposed daily to 13 hours of daylight, whereas Early Yellow Globe, Mountain Danvers, Ohio Yellow Globe, Australian Brown, White Portugal, Southport Yellow Globe, and Sweet Spanish (S1) required 13.5 hours of daylight to produce 100 percent of good bulbs. The last three varieties required longer to mature at 13.5 hours' exposure than the first four varieties. For complete bulbing of Red Wethersfield, Southport Red Globe, and Italian Red, 14 hours' exposure was necessary, whereas Yellow Globe Danvers required 14.25 hours of daylight for all of the plants to produce good bulbs.

1935 EXPERIMENT

MATERIALS

In order to extend the scope of the 1935 trials, a collection of varieties and strains of onions from Europe (table 7) was obtained from one Polish and two Dutch seedsmen. Seed of a strain of the Sweet Spanish variety was supplied by a firm of commercial seed growers at Rocky Ford, Colo. Most of the varieties supplied by the

European seedsmen are reputed to be the most important varieties in use in the northern sections of Europe. Flat Madeira and Round Madeira are varieties commonly grown in Italy and other Mediterranean countries.

The approximate latitude of the regions in which the different varieties and strains of seed were grown and the length of day in hours of possible sunlight are given in table 7.

TABLE 7.—*Varieties and strains of onions used in 1935, the approximate latitude of the region in which the seed was grown, and the longest day of possible sunlight during the growing season for each locality*

Variety and strain	Seed grown in vicinity of—	Approximate latitude	Longest day of possible sunlight
		°*N.*	*Hours*
Wolska	Warsaw, Poland	52	16.7
Yellow Rijnsburg	Central Netherlands	52	16.7
Yellow Zwijndrecht	do	52	16.7
Yellow Flat Dutch (81) [1]	do	52	16.7
Bloodred Flat Dutch (81)	do	52	16.7
Zittau Yellow	Amsterdam, Netherlands	52	16.7
Zittau Red	Halle, Germany	51	+16.5
Yellow Zittau	Central Germany	51	+16.5
Yellow Flat Giant	Wurtemburg, Germany	49	16.2
Yellow Flat Dutch (82)	Anjou, France	47	15.9
Bloodred Flat Dutch (82)	do	47	15.9
Yellow Flat Dutch (83)	Avignon, France	44	15.5
Round Madeira	Naples, Italy	41	15.1
Flat Madeira	do	41	15.1
Sweet Spanish (82) (Valencia)	Rocky Ford, Colo.	39	14.9

[1] S followed by a number indicates a separate strain.

METHODS

Seed was sown in the greenhouse at the Arlington Experiment Farm, March 2, 1935, and emerged from the soil in about 7 days. The seedlings when transplanted to the experimental boxes, May 1 and 2, were only about 3 inches tall and most of them had only the seedling leaf and one or two lateral roots. Weather conditions following transplanting were very favorable and the young plants grew rapidly. The plants were spaced 2 inches apart in the rows which were 3 inches apart. The plant boxes were 10 by 10 by 36 inches, inside measurements, and were filled with a rich compost to which a liberal application of 5–8–5 commercial fertilizer was added. One inch of muck soil constituted the upper layer of soil. Weekly applications of the above-mentioned fertilizer and nitrate of soda were made until bulb formation on the earlier maturing lots was complete.

For each variety there were 10 or 15 plants in each of the 10-, 12-, 13-, and 14-hour lots and 20 plants in the control (normal-day), 16-, and 18-hour lots. The order of planting of varieties in the replicate boxes was varied in order to minimize any possible varietal competition effects.

Insects and diseases were controlled by weekly spray applications, and excellent growth was made considering the late date of planting and the space available per plant.

The 1934 schedule and method of moving the material on trucks in and out of the dark chambers for the 10-, 12-, 13-, and 14-hour lengths of day were followed in 1935. Electric illumination (fig. 6) was used

to secure the 16- and 18-hour periods of light. The plants were placed under these treatments on June 11 and were harvested on August 17. With sunrise as the starting point for the daylight period, the lights were turned on one-half hour before sunset and continued for such time as would give 16 or 18 hours' light; 200-watt gas-filled tungsten bulbs were spaced 3 feet apart and maintained at a level of 2 feet above the ground surface of the boxes throughout the experimental period. Each group of plants was screened from the

FIGURE 6.—Arrangement of 200-watt gas-filled tungsten lights and reflectors in the 16- and 18-hour treatments in the 1935 length-of-day experiments with onions.

light of the other group by a partition high enough to cut off the direct rays of light.

A comparison of the temperatures for 1935 with those of 1934 (table 1) shows that for comparable calendar periods the season of 1935 was cooler than that of 1934.

RESULTS

During the early part of the season of 1935 no marked differences were noted in the vegetative growth rate of the onion plants under the different periods of light. By the middle of July, however, growth of the foliage of most of the varieties in the 16- and 18-hour lots had practically ceased, and some of the tops in the 18-hour lot had fallen over. The condition of the foliage on August 8 is shown in figure 7, and table 8 gives the percentage of each of three conditions of the foliage. Figure 7 shows in general more breaking over of the blades, more softening and collapse of the necks, and more desiccation of the blades

FIGURE 7.—Condition of foliage August 8, 1935, in 12 strains or varieties of onions grown at Arlington Experiment Farm under different daily periods of normal daylight as indicated: *A*, 10 hours; *B*, 12 hours; *C*, 13 hours; *D*, 14 hours; *E* (control), normal day length (12.4–14.9 hours); *F*, 16 hours; *G*, 18 hours. Small letters refer to following varieties and strains: *a*, Zittau Yellow; *b*, Yellow Rijnsburg; *c*, Yellow Flat Giant; *d*, Yellow Flat Dutch (S3); *e*, Bloodred Flat Dutch (S1); *f*, Yellow Zwijndrecht; *g*, Round Madeira; *h*, Wolska; *i*, Zittau Red; *j*, Yellow Zittau; *k*, Yellow Flat Dutch; *l*, Sweet Spanish (S2). Cross lines on the background are 12 inches apart. Note the effect of longer light periods in the collapse of the necks and desiccation of the foliage. Lateness of maturity of Round Madeira and Sweet Spanish (S2) is shown by succulence of necks and foliage in the 16- and 18-hour lots.

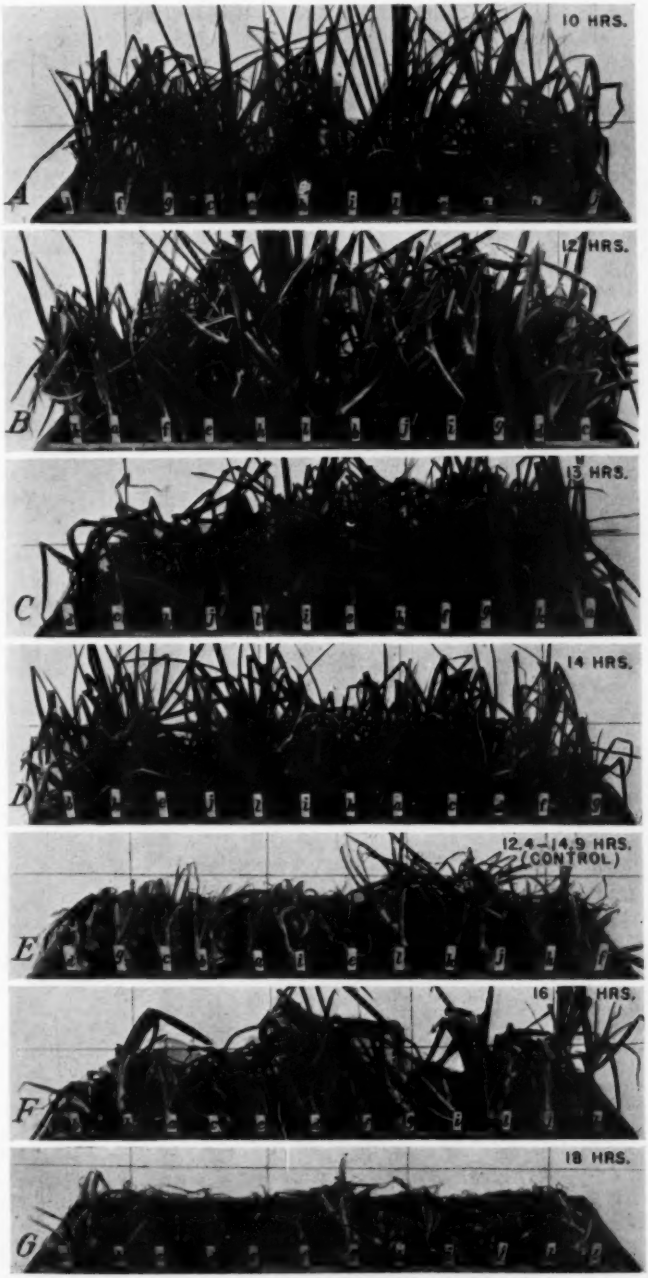

FIGURE 7.—(For explanatory legend see opposite page.)

and necks as the length of light period was increased from 12 to 18 hours daily. No measurements were made, but it was apparent that the diameter of the plants 2 inches above the ground was greater in the 12-hour lot than in the 10-hour lot.

Since the three categories of condition of foliage given in table 8 are successive stages in maturity, it is evident that increasing the length of the light period hastened the maturity of all varieties and strains. The differences between varieties and strains were not so great as in the 1934 work, but it is apparent that Sweet Spanish and Round Madeira are the latest maturing varieties in this collection. Yellow Flat Giant matured slightly earlier than the remainder of the varieties. The differences in earliness between the remainder of the strains or varieties were not very great nor very consistent in the different lots. The data from the 14-hour and the 12.4- to 14.9-hour lots indicate that Bloodred Flat Dutch (S2) is earlier maturing than Bloodred Flat Dutch (S1), but the results from the 16- and 18-hour lots indicate that the reverse is true.

TABLE 8.—*Condition of foliage on Aug. 5, 1935, in 15 varieties and strains of onions exposed to different lengths of day*

Variety and strain	Condition of foliage after daily exposure to indicated number of hours of light												
	10	12	13	14		12.4–14.9			16			18	
	Erect and green [1]	Erect and green	Erect and green	Erect and green [1]	Prostrate and green [2]	Erect and green [1]	Prostrate		Erect and green [1]	Prostrate		Prostrate	
							Green [2]	Dry [3]		Green [2]	Dry [3]	Green [2]	Dry [3]
	Pct.	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*
Sweet Spanish (S2) [4]	100	100	100	73	27	65	35	0	28	72	0	100	0
Flat Madeira	100	100	100	100	0	6	94	0	0	93	7	84	16
Yellow Flat Giant	100	100	100	50	50	0	70	30	0	33	67	15	85
Bloodred Flat Dutch (S2)	100	100	100	60	40	5	90	5	0	83	17	75	25
Yellow Flat Dutch (S2)	100	100	100	100	0	5	74	21	0	89	11	65	35
Yellow Flat Dutch (S1)	100	100	100	80	20	0	94	6	0	70	30	47	53
Yellow Flat Dutch (S3)	100	100	100	100	0	65	29	6	0	85	15	31	69
Yellow Rijnsburg	100	100	100	93	7	33	67	0	0	47	53	45	55
Round Madeira	100	100	100	83	17	20	80	0	6	94	0	94	6
Wolska	100	100	100	100	0	69	31	0	0	75	25	40	60
Yellow Zwijndrecht	100	100	100	93	7	47	47	6	0	90	10	55	45
Bloodred Flat Dutch (S1)	100	100	100	100	0	37	63	0	0	65	35	22	78
Zittau Yellow	100	100	100	100	0	40	55	5	0	75	25	56	44
Zittau Red	100	100	100	100	0	42	58	0	0	74	26	55	45
Yellow Zittau	100	100	100	100	0	53	35	12	0	67	33	58	42

[1] Petiole column erect and majority of leaves green and succulent.
[2] Petiole column flaccid and bent over and one or more leaves green and succulent.
[3] Petiole column flaccid and bent over and all the leaves dry or nearly so.
[4] S followed by a number indicates a separate strain.

In order to prevent the bulbs from rotting in the early-maturing treatments, all plants whose tops had fallen over were pulled on August 17 and cured under cover. The remainder of the lots were harvested on September 6 and graded, as in 1934, into scallions, bottlenecks, or good bulbs. Representative portions of 12 of the strains from the 12-, 13-, 14-, and 12.4- to 14.9-hour lots are shown in figures 8 and 9.

The data in table 9 show that none of the varieties was able to form any good bulbs or bottlenecks with 10 hours of daylight daily, whereas all of the varieties produced 100 percent of good or normal bulbs with

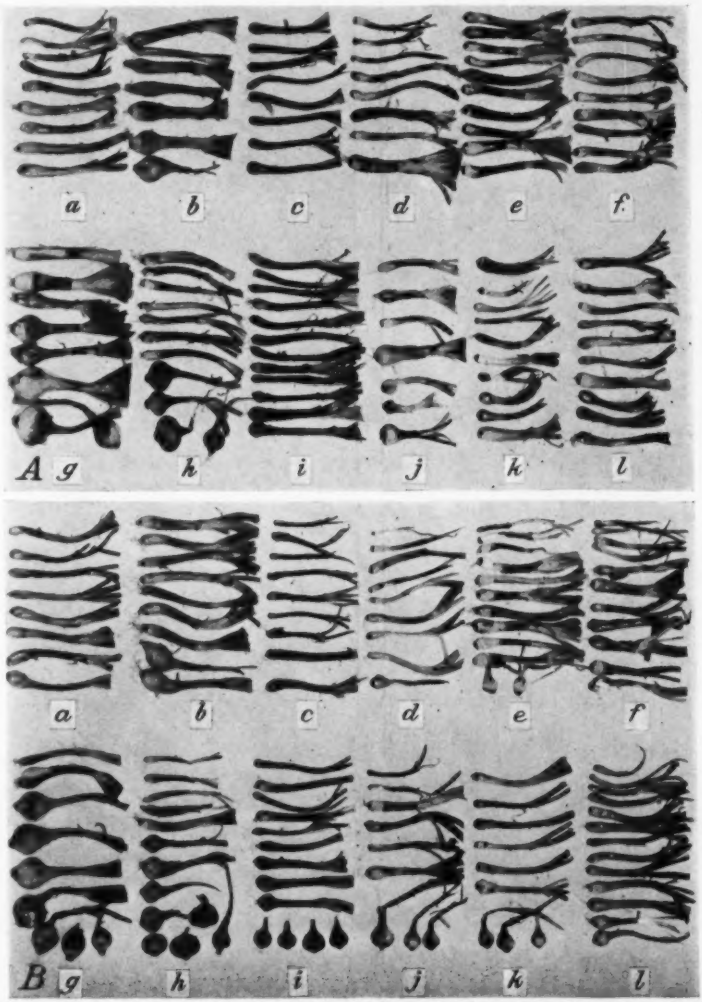

FIGURE 8.—Degree of bulbing of onions in 1935 when exposed to (*A*) 12 hours of daylight daily and (*B*) 13 hours. Representative group of plants from 12 strains or varieties: *a*, Wolska; *b*, Round Madeira; *c*, Blood-red Flat Dutch (S1); *d*, Zittau Yellow; *e*, Yellow Flat Dutch (S2); *f*, Yellow Rijnsburg; *g*, Sweet Spanish (S2); *h*, Flat Madeira; *i*, Bloodred Flat Dutch (S2); *j*, Yellow Flat Giant; *k*, Yellow Flat Dutch (S3); *l*, Yellow Zwijndrecht. Compare with figure 9 and note general increase in percentage of good bulbs in longer lighted periods. Also note differences in strains *c* and *i* and *e* and *k*.

16 or 18 hours of light. Sweet Spanish (S2) Flat Madeira, and Yellow Flat Giant were able to make a small percentage of good bulbs in the 12-hour lot. It required a minimum of 13 hours of light to

produce normal bulbs in the Bloodred Flat Dutch (S2) Yellow Rijnsburg, Wolska, and all three strains of Yellow Flat Dutch varieties.

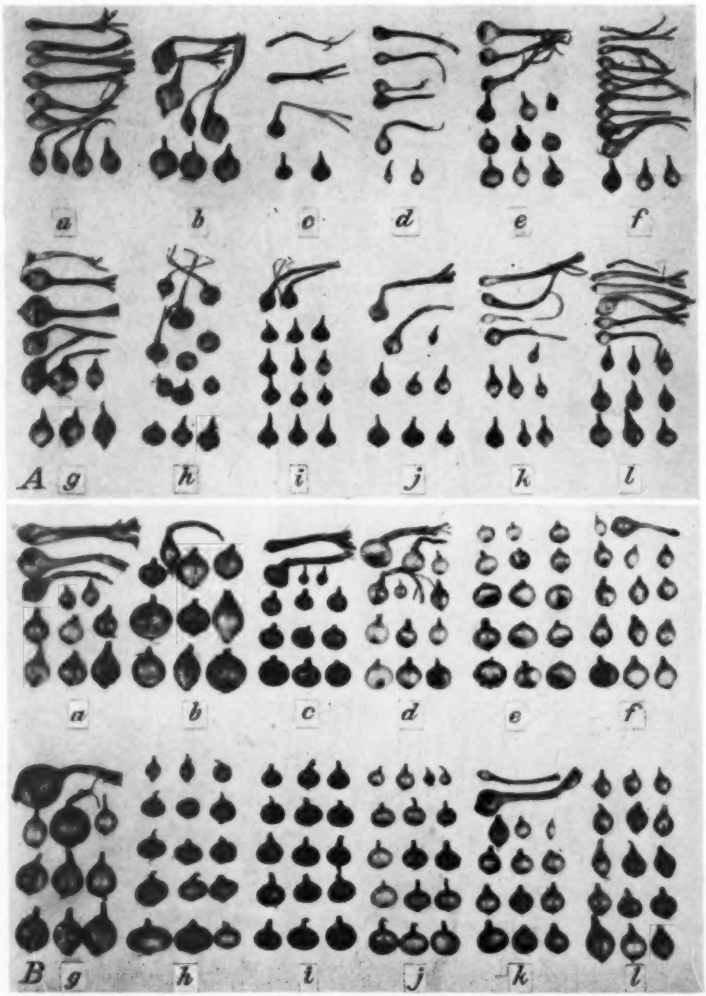

FIGURE 9.—Degree of bulbing of onions in 1935 when exposed to (*A*) 14 hours of daylight daily and (*B*) the normal variation in day length at Washington, D. C. (12.4–14.9 hours). Representative group of plants from 12 strains or varieties: *a*, Wolska; *b*, Round Madeira; *c*, Bloodred Flat Dutch (S1); *d*, Zittau Yellow; *e*, Yellow Flat Dutch (S2); *f*, Yellow Rijnsburg; *g*, Sweet Spanish (S2); *h*, Flat Madeira; *i*, Bloodred Flat Dutch (S2); *j*, Yellow Flat Giant; *k*, Yellow Flat Dutch (S3); *l*, Yellow Zwiindrecht. Compare with figure 8 and note general increase in percentage of good bulbs in the longer lighted periods.

Round Madeira, Yellow Zwijndrecht, Bloodred Flat Dutch (S1), Zittau Yellow, Zittau Red, and Yellow Zittau required 14 hours of daylight for the production of any good bulbs.

TABLE 9.—*Degree of bulb formation in 15 varieties and strains of onions exposed to different lengths of day in 1935*

Variety and strain	Bulb formation after daily exposure to indicated number of hours of light														
	10	12			13			14			Normal (12.4–14.9)			16	18
	Scallions	Good bulbs	Bottlenecks	Scallions	Good bulbs	Bottlenecks	Scallions	Good bulbs	Bottlenecks	Scallions	Good bulbs	Bottlenecks	Scallions	Good bulbs	Good bulbs
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Sweet Spanish (82)[1]	100	28.6	35.7	35.7	76.9	7.7	15.4	93.3	0.0	6.7	100.0	0.0	0.0	100	100
Flat Madeira	100	21.4	7.1	71.5	38.5	15.4	46.1	100.0	.0	.0	100.0	.0	.0	100	100
Yellow Flat Giant	100	12.5	25.0	62.5	33.3	.0	66.7	88.9	11.1	.0	100.0	.0	.0	100	100
Bloodred Flat Dutch (82)	100	.0	.0	100.0	30.8	7.7	61.5	100.0	.0	.0	100.0	.0	.0	100	100
Yellow Flat Dutch (82)	100	.0	.0	100.0	15.4	15.4	69.2	91.7	8.3	.0	100.0	.0	.0	100	100
Yellow Flat Dutch (81)	100	.0	.0	100.0	10.0	.0	99.0	80.0	10.0	10.0	100.0	.0	.0	100	100
Yellow Flat Dutch (83)	100	.0	.0	100.0	33.3	11.1	55.6	63.7	9.0	27.3	88.9	11.1	.0	100	100
Yellow Rijnsburg	100	.0	.0	100.0	9.1	.0	90.9	46.1	23.1	30.8	94.2	5.8	.0	100	100
Wolska	100	.0	.0	100.0	12.5	.0	87.5	40.0	40.0	20.0	82.4	11.7	5.9	100	100
Round Madeira	100	.0	10.0	90.0	.0	20.0	80.0	100.0	.0	.0	94.5	5.5	.0	100	100
Yellow Zwijndrecht	100	.0	.0	100.0	.0	.0	100.0	60.0	20.0	20.0	100.0	.0	.0	100	100
Bloodred Flat Dutch (81)	100	.0	.0	100.0	.0	.0	100.0	60.0	.0	40.0	89.4	5.3	5.3	100	100
Zittau Yellow	100	.0	.0	100.0	.0	.0	100.0	75.0	12.5	12.5	94.7	5.3	.0	100	100
Zittau Red	100	.0	.0	100.0	.0	.0	100.0	70.0	20.0	10.0	79.0	15.7	5.3	100	100
Yellow Zittau	100	.0	.0	100.0	.0	.0	100.0	40.0	10.0	50.0	88.9	11.1	.0	100	100

[1] S followed by a number indicates a separate strain.

Most of the varieties in this test were more variable in their response to length of day in bulb formation than those in the 1934 test. For instance, the Wolska variety contained some individuals that were able to produce good bulbs with 13 hours of light and others that required more than 14.9 hours. Bloodred Flat Dutch (S2) and Yellow Zwijndrecht were very uniform with respect to their reaction to length of day.

Of the 15 varieties and strains, only 7, Sweet Spanish (S2), Flat Madeira, Yellow Flat Giant, Bloodred Flat Dutch (S2), Yellow Zwijndrecht, and Yellow Flat Dutch (S1) and (S2), were able to produce 100 percent of good bulbs under the most favorable growth conditions and normal length of day at Arlington, Va. (maximum 14.9 hours). The other eight strains therefore require more than 14.9 hours to produce a crop of normal bulbs. Flat Madeira and Bloodred Flat Dutch (S2) were able to produce 100 percent of normal bulbs with 14 hours of light.

The two strains of the Bloodred Flat Dutch showed remarkable differences in their reaction to length of day. S2 produced 30.8 percent of good bulbs in the 13-hour lot and 100 percent of good bulbs in the 14-hour treatment whereas S1 produced no good bulbs in the 13-hour treatment and required more than 14.9 hours of light to produce 100 percent of normal bulbs. Differences were not so marked in the strains of Yellow Flat Dutch, but it is apparent that S3 was not as uniform in its reaction to length of day as were the other two strains, for although it contained a greater percentage of plants capable of normal bulb production with 13 hours of light than the other two strains, it also contained some plants that required more than 14.9 hours of light to produce normal bulbs.

The number of splits and doubles was smaller in the 1935 material than in the 1934 material, probably because of less favorable growth conditions in 1935 (late planting and thickness of planting). Round Madeira was the most susceptible variety and had one split in the 12-hour lot, two splits in the normal-day lot, one double in the 16-hour, and two doubles in the 18-hour lot. Wolska produced one split in the 10-hour lot and two doubles in the 16-hour lot. Yellow Zittau had one double in the 16-hour lot and Yellow Flat Dutch (S3) had one split in the 12-hour lot. With such small numbers there is no apparent correlation between treatment and number of doubles and splits. Under lengths of day unfavorable for normal bulbing, splits are produced; and under lengths of day favorable for bulb formation the outer skin splits to the base, resulting in doubles.

DISCUSSION

In general, the foregoing results agree with those of other investigators who have worked with the same varieties of onions, although there are some exceptions, due possibly to the different environmental conditions under which the material was grown or to inherent differences in the strains used. Although strains of varieties are known to differ sometimes as much as closely related varieties, it is possible that the varieties or strains of Bermuda onions that were grown by the different workers were all of the same general type, differing mainly in color, since the majority of seed of this type is grown on the Canary Islands. The area of these islands is so limited and the climate is so

uniform that there is very little likelihood of the development of strains differing widely in physiological characteristics. There is a possibility that McClelland (*6*) was working with the same type as were the writers, for White Bermuda and Yellow Bermuda are frequently considered synonymous by the seed trade. The results of McClelland with White Bermuda, those of the writers with Yellow Bermuda, and those of Beattie and Allard [3] with Red Bermuda at Arlington Experiment Farm in 1930 agree in that no normal bulbs developed when the plants were exposed to only 10 hours of light. The results given herein and those of Beattie and Allard indicate that normal bulbs may be produced at 12 hours' light duration or longer. McClelland did not have a 12-hour treatment, but found no normal bulbs at 11 hours' exposure to light; however, normal bulbs were produced at normal light exposures that ranged from 11.2 to 13.2 hours.

Bos (*2*), working with many strains of Silberzwiebel, no doubt had in his cultures the type that the writers and Garner and Allard (*3*, *4*) have grown under the names Silverskin and White Portugal, which are synonyms in the United States. Since Bos was unable to get bulbs at 12-hours' light exposure, it is probable that he did not have the white-skinned Bermuda type in his material. In his experiments a light exposure of 14 to 15 hours' duration produced good bulbs. Garner and Allard did not have a 12-hour treatment, but their results are in agreement with those of the present work in that they did not get good bulbs at 5 or 10 hours but did get normal bulbs at light exposures of 13 hours or longer.

Yellow Globe as a varietal name for onion usually refers to the Southport Yellow Globe variety, although it also may be used for the Yellow Globe Danvers variety. The results of the present work, however, indicate that both varieties have essentially the same minimum light requirement (13 hours) for bulb formation, although neither produced 100 percent of good bulbs at this exposure. In the normal day (11.2 to 13.2 hours) and with 13.5 hours' exposure to light, McClelland (*6*) secured good bulbs, but it was 50 weeks before the tops fell over. Under 15 hours of light the bulbs had formed or were forming at 25 weeks. The photographs of the Yellow Globe variety in the Beattie and Allard [4] records show that although none of the tops of the onions in the 13-hour lot had fallen over, bulb formation was well advanced, and doubtless most of the plants would have matured normally if they had been allowed to grow longer. This situation would be the same as found in the present work at a comparable stage of development. Therefore 13 hours would seem to be the minimum exposure for bulb formation of all Yellow Globe varieties; but to insure that all the plants make good bulbs and to shorten the time required for bulbing, a longer light exposure is required for these varieties.

In Wilson's work (*8*) the failure of the Yellow Strasburg variety to bulb when grown in early spring, during a period when the length of daylight varied from 12.2 to 14.2 hours, may have been due to low intensity of light during the spring in the greenhouse at Ithaca, N. Y., or to the unusual conditions of growth in water cultures. The same reasons may be advanced for the failure of many of the plants of the Ebenezer variety to bulb in the winter, although artificial light was

[3] BEATTIE, J. H., and ALLARD, H. A. Unpublished data.
[4] BEATTIE, J. H., and ALLARD, H. A. (See footnote 3.)

supplied from 5 p. m. to 10 p. m. each day, making the total light period from 14.3 to 15.3 hours during the course of the experiment. Yellow Strasburg produced good bulbs in water culture when grown from June 12 to July 15 (14.9 to 15.3 hours of possible daylight) in the greenhouse. This would seem to argue that the conditions of nutrition in water culture were not entirely responsible for the failure of the spring crop.

Yellow Strasburg is also known in the seed trade as Yellow Dutch and is the same color and shape as the strains of Yellow Flat Dutch used in the 1935 experiment. The results in tables 6 and 10 indicate that the American-grown strain had the same minimum day length for bulbing (13 hours) but was more uniform in bulbing and matured all of its bulbs at a shorter day length than the European strains.

Valencia, Prizetaker, and Sweet Spanish, if not always synonyms, refer to the same general type. Beattie and Allard's results [5] with Valencia and the 1934 results of the present work with Sweet Spanish both show 13 hours to be the minimum light exposure (of those studied) for bulb formation and that longer periods of light are necessary for the production of 100 percent of good bulbs. In McClelland's work the results with Prizetaker are not as clear-cut, for only a few bulbs were formed in the 13.5-hour and normal-day (11.2 to 13.2 hours) lots, whereas for the majority of the plants McClelland states that the "stage of development appeared to be intermediate between that of spring onions and matured bulbs." In the work reported herein, the 1935 results with the Colorado strain of Sweet Spanish (S2) differed from the results of 1934 with the Utah strain (S1) in that the Colorado strain was more variable in its reaction to length of day than the Utah strain, containing some plants capable of bulb production with only 12 hours of light daily and other plants that required more than 14 hours of light daily.

The 1935 data (table 8) also show differences and similarities in reaction between strains of the same variety. As previously pointed out, the most striking difference is found between strains 1 and 2 of Bloodred Flat Dutch. Strain 2 was earlier in maturing in the 14-hour and normal-day lots but slightly later in the 16- and 18-hour lots than strain 1. Strain 2 was also able to produce bulbs on all its plants at a shorter light period than strain 1. The data in table 6 show that strain 2 was grown in a locality where the maximum length of day is shorter than that in the locality where strain 1 was grown. Strains of Yellow Flat Dutch grown at the same locations, however, do not show as much difference as the strains of Bloodred Flat Dutch. Yellow Zittau and Zittau Yellow, from the same general latitude, do not differ in their reaction to length of day.

Variability in bulb formation within a variety is probably an expression of the constitution of the variety as a whole with respect to the bulb-formation factor or factors. It is evident that not as much attention has been paid by the onion-seed growers to attaining uniformity in this character, which appears in the field as earliness of maturity, in the late varieties as in the early ones.

These results also agree with those of other workers in that all varieties and strains tested have reacted in the same way toward length of day. The varieties and strains have been shown to have

[5] Beattie, J. H., and Allard, H. A. (See footnote 3.)

very definite minimum day lengths at which bulb formation may take place, but increasing the light duration beyond this minimum has invariably increased the rate of maturity for successive increments of light in all varieties and strains tested.

In addition to showing that varieties are inherently different in their response to length of day, and that this response is a very important factor in bulb formation, the data illustrate the influence of environmental factors on the expression of genetic factors. In the 1934 experiment California Early Red, Yellow Strasburg, Ebenezer, and Yellow Danvers Flat produced 100 percent of scallions with 12 hours of light daily, whereas they produced 100 percent of good bulbs with 13 hours of light daily. It seems remarkable that 1 additional hour of light per day should be able to effect such a change in the expression of the genotype.

Cognizance should be taken of the possible effect of other factors on bulb formation. Unfortunately no definite information is available on the interrelation of many factors, such as duration and intensity of light, effect of twilight periods on plant growth, nutritional elements and levels, soil moisture, and temperature of both soil and air on the onion plant. In the evidence that is available the number of varying factors is usually small, but the data are suggestive in pointing out reasons why field tests or tests conducted under different conditions may not give the same results. Temperature of the soil and air has been shown by Walker and Jones (*7*) to have a pronounced effect on the growth rate of onion seedlings. They not only found that roots and foliage had different optimum temperatures for growth but that varieties also differed in their temperature optima. Red Globe made the largest root growth at a soil temperature of 57.2° F. and Yellow Bermuda at 68°. Maximum top growth for Red Globe occurred at a soil temperature of 68° and for Yellow Bermuda at 77°. The air temperature varied from about 60° at night to as high as 85° during the middle of the day. Germination and growth were very slight at a soil temperature of 95°. Wilson's (*8*) work, however, shows that high temperatures do not prevent the bulbing of the Yellow Strasburg variety, although Garner and Allard (*4*) found that onions grown in the greenhouse in the summer were smaller than those grown outside at the same time. The extremely small size of White Creole in the 1934 experiment may have been due to its sensitiveness to temperature, which was higher than in its native region at the bulb-formation period. The difference in behavior between the Wolska variety in the field in 1934 and the same strain in boxes in 1935 may have been due to more root growth in the field because of lower soil temperatures or to a nitrogen shortage in the soil at the time bulb formation should have taken place. Wilson points out that nitrogen-starved plants are characterized by a stunted growth, rigidly erect position of the leaves, and a failure of the roots to die at the same time as those of normal plants. No nitrogen fertilizer was applied after the foliage of the early-maturing varieties started to fall over, and it is entirely possible that the surrounding varieties may have depleted the soil of its soluble-nitrogen content before the daylight period was long enough for bulb formation to take place. Extensive injury to the foliage by thrips doubtless was a factor in the field results.

PRACTICAL CONSIDERATIONS

These results on length of day as a factor in the bulb formation of onions give a good clue to some of the reasons for the regional importance or adaptability of some varieties. Only rarely has anyone in the major northern storage-onion-growing sections of the United States been able to obtain a satisfactory yield from the Bermudas, Early Grano, or Creole by sowing the seed in the field at the usual date for main-crop varieties. Planting in the Northern States is usually done at a time when the length of day has already passed the minimum for bulbing and is very rapidly increasing. Under such conditions these varieties make only a few leaves and then form bulbs that are usually little more than sets in size.

The failure of varieties commonly used in the northern onion-growing sections of the United States when grown in the Tropics or in regions where the length of day is less than 13 hours may be partially explained on the length-of-day basis. Wilson (*8*) cites correspondence with workers in Java who report failure of onions to mature even at the cooler and higher altitudes. The failure of most storage varieties of onions to bulb properly when grown at Winterhaven, Tex., during 1933, 1934, and 1935 cannot be attributed solely to length of day, since the maximum length of daylight reaches 14.1 hours, which, according to the present work, is sufficient for good bulb formation and maturity.

Temperature in itself can hardly be considered the critical factor in this instance, since temperatures in the northern onion-growing sections equal and frequently exceed those encountered during the growing season in this Texas section; indirectly, however, it probably plays a very important part. It is well known that high temperatures increase the damage from pink root and thrips when these pests are present. In 1933 both pests were present in the Texas planting. Early-maturing varieties such as the Bermudas, Creoles, and Early Grano, suffered no appreciable damage, as the high temperatures favoring the development of the pests occurred after these plants had made the major part of the bulb growth. The later maturing varieties, however, had just entered the bulbing period of growth, and the combined loss of roots, due to pink root, and of foliage, due to thrips, prevented normal development of the plant even though length of day was favorable. In 1934 and 1935, when pink root was not so prevalent as in 1933, Sweet Spanish and Prizetaker were able to produce a large percentage of normal bulbs. These varieties are more resistant to attack by thrips than the other late-maturing varieties in this experiment, and for this reason were able to produce good bulbs.

The Wolska variety, when grown in the field at Arlington Experiment Farm in 1934, failed to make normal bulbs; the necks did not soften, and new leaves continued to form long after the American varieties were harvested. When grown in the length-of-day experiments in 1935, 82.4 percent of the plants produced normal bulbs with normal day length. The failure of the 1934 crop to produce bulbs may have been partly due to the damage inflicted by a severe infestation of thrips, which killed most of the larger leaves. The loss of these leaves may have prevented the elaboration and accumulation of sufficient photosynthates to accomplish bulb formation, even though the length of day was favorable for bulb formation. This may also be

the explanation for the failure of northern European varieties in our northern onion-growing sections. The formation of the bulbs is delayed so late in the season by their photoperiod requirement that unfavorable growth conditions, such as extreme heat, drought, disease, and insect damage, prevent bulb formation.

In arranging a planting schedule, a knowledge of the length of day required for bulb formation of varieties currently offered for sale is also important in order to get the best results. There is a high correlation between the size of plant at the date when bulbing starts and the size of the mature bulb. It also has been demonstrated that the age of the plant has little influence on date of maturity; that is, seed sown the same date on which plants 3 months old are set will mature bulbs within 5 days of the date at which the bulbs from plants mature, and the bulbs from seed will be much smaller than those from plants. Thus, earlier sowing (within limits) results in larger yields both in the South and the North because the plant has a longer time in which to make vegetative growth and therefore has reached a larger size when length of day begins to exert its influence in the formation of the bulb. For the same reason early-maturing varieties make larger yields when sown early. If planting should be delayed for some reason, what choice should the grower make as to variety in order to secure the greatest yield? Provided the growing season was long enough, it would seem logical to select one of the varieties that do not react so quickly to length of day, i. e., one of the later maturing varieties. Knott (*5*), working in New York, found a positive correlation between yield and the lateness of maturity of the varieties studied.

The matter of varietal season of maturity seems to depend (1) on response of the variety to the length of day and (2) on its rate of development under each day length that is longer than the minimum required for bulb formation. The varieties in table 3 may be divided into two main groups, the first being composed of the first three varieties that were capable of bulb formation under a photoperiod of 12 hours or less and the second of those that were able to produce bulbs at a photoperiod of 13 hours. Within this latter group, however, there were marked differences in the dates at which the varieties matured. Thus, although in this experiment Ebenezer and Sweet Spanish both produced good bulbs at every exposure beyond 12 hours, Ebenezer matured in advance of Sweet Spanish in each photoperiod beyond 12 hours. The difference in number of days was not determined in this experiment, but when grown under the normal length of day in the field in 1934 Ebenezer was ready to harvest 22 days before Sweet Spanish. In general, the maturity groups based on the field results agree rather closely with those given in the discussion of table 3. It is also of interest to point out that the first three varieties in table 3 have been developed in or are adapted to the most southern parts of the United States, whereas the larger group has been developed in and adapted to the States north of the thirty-eighth parallel.

In the 1935 results there are three groups of varieties with regard to the minimum length of day required for bulbing (table 8). Sweet Spanish, Flat Madeira, and Yellow Flat Giant required only 12 hours of light, Bloodred Flat Dutch (S2), the three strains of Yellow Flat Dutch, Yellow Rijnsburg, and Wolska required 13 hours, and Round Madeira, Yellow Zwijndrecht, Bloodred Flat Dutch (S1), and the

Zittau strains all required 14 hours to produce any good bulbs. In each of these groups there were also marked differences in the time at which the plants matured, although the differences were not so great as in the 1934 experiment. In the first group mentioned above, Sweet Spanish was the latest maturing; it was also later maturing than any of the other strains in the trial. Round Madeira was next in lateness of maturity, as the data in table 8 indicate. Earliness of maturity seems to depend upon the ability to start bulb formation at short photoperiods and to proceed very rapidly with the process after the minimum photoperiod for bulbing is reached. Lateness of maturity may be due to a long photoperiod requirement or to a slow rate of bulb development at superminimal photoperiods or to a combination of these two conditions.

The success or failure of an introduced onion variety in any new location probably can be fairly accurately foretold by comparing the length and the photoperiod of the growing season of its native home with those of the region into which it is to be introduced.

Growing varieties of onions under the various photoperiods, as the writers have done, serves to indicate not only the relation of bulb formation in the variety to the most favorable photoperiod but also the purity of the stock in its response to length of day.

The photographs showing the degree of bulbing of the varieties under the different exposures to daylight (figs. 2 to 5) are of interest in this connection. It will be noted that the Yellow Danvers Flat, the Yellow Strasburg, and the California Early Red, for instance, showed no bulbing under the 12-hour day but developed good bulbs on all the plants grown under the 13-hour day. In the Australian Brown, the Mountain Danvers, the Ohio Yellow Globe, the Early Yellow Globe, and the White Portugal, some plants bulbed well and rapidly under the 13-hour day whereas others did not bulb. It would appear that the varieties of the second group were not quite so pure in their length-of-day adaptations as those of the first group. It is evident that these variations of behavior become most pronounced around the critical minimum photoperiods at which bulbing takes place for the variety in question. This suggests that selection for purity of type or for producing an earlier or later strain of any variety would prove more feasible when the plants were grown, so that their bulbing behavior could be observed around the critical length of day or photoperiod at which bulbing naturally begins.

SUMMARY

In 1934 tests were conducted at the Arlington Experiment Farm, Arlington, Va., with 18 of the most important American varieties of onions under normal intensities of daylight at exposures of 10, 12, 13, 13.5, 14, and 14.25 hours and normal day length (12.4 to 14.9 hours). In 1935, tests were made with 11 varieties, 10 European and 1 American, grown with daylight exposures of 10, 12, 13, and 14 hours, normal day length, and with photoperiods in which electric illumination supplemented the normal daylight to give 16 and 18 hours of light daily.

Increasing the length of photoperiod hastened the maturity of all varieties studied.

Varieties and strains differed markedly in the minimum photoperiod required for bulb formation and in the rate and uniformity of bulb

formation at superminimal photoperiods. Yellow Bermuda was the only variety that produced normal bulbs (10 percent) in the 10-hour treatment. Yellow Bermuda, White Creole, Early Grano, Early Yellow Globe, Flat Madeira, Yellow Flat Giant, and Sweet Spanish (S2) produced some normal bulbs in the 12-hour treatment. Varieties that produced one or more good bulbs in the 13-hour treatment were California Early Red, Yellow Strasburg, Ebenezer, Mountain Danvers, Ohio Yellow Globe, Yellow Danvers Flat, Australian Brown, Red Wethersfield, White Portugal, Yellow Globe Danvers, Southport Red Globe, Southport Yellow Globe, Italian Red, Sweet Spanish (S1), Bloodred Flat Dutch (S2), Yellow Flat Dutch (S1, S2, and S3), Yellow Rijnsburg, and Wolska. Round Madeira,[6] Yellow Zwijndrecht,[6] Zittau Yellow,[6] Bloodred Flat Dutch (S1),[6] Yellow Zittau,[6] and Zittau Red[6] required 14 hours light to produce any good bulbs.

The shortest photoperiods required to produce 100 percent of normal bulbs in the different varieties and strains were as follows:

12 hours.—Yellow Bermuda, White Creole, and Early Grano.
13 hours.—California Early Red, Yellow Strasburg, Ebenezer, and Yellow Danvers Flat.
13.5 hours.—Early Yellow Globe, Mountain Danvers, Ohio Yellow Globe, Australian Brown, White Portugal, Southport Yellow Globe, and Sweet Spanish (strain 1).
14 hours.—Red Wethersfield, Southport Red Globe, Italian Red, Flat Madeira, Round Madeira, and Bloodred Flat Dutch (S2).
14.25 hours.—Yellow Globe Danvers.
Normal day (maximum, 14.9 hours).—Yellow Flat Giant, Yellow Flat Dutch (S1), Yellow Zwijndrecht, Yellow Flat Dutch (strain 2), Sweet Spanish (strain 2).
16 hours.—Bloodred Flat Dutch (S1), Yellow Flat Dutch (strain 1), Yellow Rijnsburg, Zittau Yellow, Zittau Red, Yellow Zittau, and Wolska.

Varietal season of maturity seems to depend (1) upon the response to length of day and (2) to the rate of development at each indicated length of day longer than the minimum required for bulb formation. Thus, although in this experiment Ebenezer and Sweet Spanish (S1), produced some good bulbs at every exposure beyond 12 hours, Ebenezer matured its bulbs before Sweet Spanish in every photoperiod beyond 12 hours. Sweet Spanish and Round Madeira were the latest maturing varieties in this experiment.

The success or failure of an introduced onion variety in any new location probably can be fairly accurately foretold by comparing the length and the photoperiod of the growing season of its native home with those of the region into which it is to be introduced.

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A COMPARISON OF SOME METHODS USED IN DETERMINING PERCENTAGE UTILIZATION OF RANGE GRASSES[1,2]

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INTRODUCTION

Perennial grasses constitute the chief forage on extensive areas of sagebrush-wheatgrass spring-fall ranges in Utah, Idaho, Nevada, and southwestern Wyoming. Since maintenance of range productivity is dependent upon the perpetuation of these grasses, sound range management must be based upon their growth requirements.

With the increasing demand for these ranges, it is essential to know and to be able to recognize accurately the proper intensity of use for each of the important grass species. Purely descriptive terms such as "light", "moderate", "heavy", "conservative", and "full" fail to meet this need in defining past or recommended use, because each term is subject to wide individual interpretation.

It was the purpose of this study to compare the accuracy of several methods for determining percentage utilization of grasses and their adaptability to the light-to-medium intensities of use essential to the maintenance of spring ranges. Since grazing removal of grasses by sheep does not differ radically from that by cattle or horses, the results here given, based on studies of sheep range, are also applicable in the main to similar ranges grazed by cattle.

Field work on this study was conducted at the United States Sheep Experiment Station located on the upper Snake River plains near Dubois, Idaho, during the fall of 1935. Vegetation in this locality is typically sagebrush-wheatgrass, in the main consisting of two species, bluebunch wheatgrass (*Agropyron spicatum*) and threetip sagebrush (*Artemisia tripartita*). Bluebunch wheatgrass forms the chief source of forage.

DESCRIPTION OF METHODS NOW IN USE

Five methods of determining percentage utilization have been used more or less commonly by range investigators in pasture and open-range studies. A sixth method included in the trial was devised during the progress of the study.

GENERAL RECONNAISSANCE

With the general reconnaissance method, the investigator inspects an area of several hundred to several thousand acres, more or less in detail, making estimates of utilization for the entire unit either for all vegetation or by individual species. These estimates are made of the

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percentages of total plant height or volume production removed by grazing. Because accuracy of such estimates varies considerably according to the individual making them, and even with the same individual at different times, some modifications of the general reconnaissance method have been tried. Chief of these is a method in which the percentage of plants grazed and percentage of grazed plants taken are estimated, the product of these two figures being regarded as percentage utilization.

MEASUREMENT

The measurement method is based on the premise that percentage utilization of grasses is equal to the reduction in average leaf height as a result of grazing. Under grazing conditions two variations of the method can be used, dependent upon the time and duration of the grazing period: (1) If grazing occurs during the period of rapid height growth of the grasses and is of such duration that growth during the intervening period is appreciable, the use of temporary enclosures is necessitated. After grazing, the difference between the average basal leaf height of grasses on several enclosures selected at random and on an equal number of grazed plots is taken to represent removal, from which percentage utilization can be calculated. (2) When grazing occurs after growth has ceased or when it is negligible during the grazing period, measurements taken at random either on plots or transects before and after grazing can be used to form the basis for the calculation of percentage utilization.

VOLUME BY WEIGHT

The volume-by-weight method, used in pasture studies by Beruldsen and Morgan (*1*),[4] is based on the assumption that percentage utilization of grasses is equal to the percentage reduction that occurs in volume by weight of herbage on an area, as a result of grazing. Use of two sets of randomized plots or transects is required for the study of degree of removal on grazing areas by this method. On one set, *A*, herbage is removed by clipping prior to grazing, or immediately after if grazing has been excluded by temporary hurdle enclosures. Herbage from the other set, *B*, left open to grazing, is removed by clipping as soon as grazing of the area has been completed. Air-dry weights of the herbage from the two series of plots are obtained. Grazing is assumed to be responsible for the difference in productivity of the two sets. Thus the reduction in productivity of the series left open to grazing, *B*, when compared to the protected, or *A*, series is expressed as utilization in percentage of the production on the *A* series. This method possesses two very desirable features, simplicity and elimination of personal error.

STEM COUNT

Stoddart (*6*) recently suggested the use of the stem-count method on ranges where *Agropyron smithii* was predominant. The stem-count method is based on the premise that percentage utilization varies directly with the percentage of the total number of stems that are grazed. It merely requires a count of grazed and ungrazed stems on randomized plots. From this count degree of utilization is

[4] Reference is made by number (italic) to Literature Cited, p. 765.

computed, using the proportion of grazed stems as the percent utilized. The stem-count method is extremely simple and nearly free from personal error.

OCULAR ESTIMATE BY PLOT

The ocular estimate-by-plot method, a modification of the general reconnaissance method, was developed and adapted for use on grasses at the United States Sheep Experiment Station in 1933. It differs from the former in that each estimate is made on a plot of such limited area that the entire plot is clearly visible from one point, and percentage utilization is the average of estimates from a series of plots selected at random. As with the general reconnaissance method, percentage utilization of height, volume, or weight is estimated. By confining observations to smaller areas, adequately replicated, rather consistent results between individual workers have been obtained. This method seems to embody four very desirable features: (1) Observations are limited to a small area, which makes possible more accurate decision; (2) errors in personal judgment on individual plots frequently tend to be compensating; (3) data thus collected can be subjected to statistical analysis; and (4) data collected from these randomized samples are valuable in studying the distribution of grazing use on range areas.

Stapledon (*5*) favors the small plot not only because it permits adequate replication for statistical purposes, but because—

> it makes you look at it as a whole—makes you concentrate attention upon it—and thus the greater your number of replications by that much the deeper and more intensive your contemplations.

OCULAR ESTIMATE BY AVERAGE OF PLANTS

The ocular-estimate-by-average-of-plants method is an additional refinement of the ocular-estimate-by-plot method, devised for grasses during the progress of the experimental study. It differs only in that percentage removal of weight is estimated for each plant within the block, or plot, and the average of these estimates is taken as percentage utilization for the plot.

CHARACTERISTICS ESSENTIAL TO A DESIRABLE METHOD

To be suitable for grazing studies conducted with a small staff, a satisfactory method of determining percentage removal of grasses should have the following qualifications:

1. Rapidity in conducting observations is necessary if enough replications are to be obtained to sample an area adequately where soil heterogeneity and differences in individual plant growth are augmented by irregularities in utilization. Slow, laborious methods prevent this adequate replication. Klapp (*3*) states that "random sampling must be repeated as much as possible, and not even the greatest accuracy in individual readings can take the place of this."

2. Accuracy not only requires minimum error in the average of several determinations, but also a close correlation between individual determinations and actual volume removal. Freedom from personal error is one of the major factors in accuracy. With studies of long duration and changing personnel, errors of individual determinations are of major importance and frequently are of such magnitude as to destroy evidence of small changes in grazing capacity.

3. Adaptability, although not a factor of material importance with grasses alone, is particularly important where studies are being conducted on vegetation composed of mixed grasses, weeds, and shrubs, and where one method must be used to obtain percentages for all groups. Methods devised for one species are not always fully desirable for others. Since in the present study but one species is dealt with, the factor of adaptability does not enter specifically, but it should be considered in a choice of methods.

EXPERIMENTAL TECHNIQUE

The accuracy, the inherent personal error, and the rapidity of the measurement, stem-count, ocular-estimate-by-plot, and ocular-estimate-by-average-of-plants methods of determining percentage utilization of grasses were tested, using an adaption of the volume-by-weight method as a base for comparison.

Only bluebunch wheatgrass was used in this study of methods because (1) it is the principal forage species in the locality; and (2) results from this species should be applicable in the main to other bunchgrasses.

A rectangular, ungrazed area, 100 by 25 feet in size, having a normally uniform cover of bluebunch wheatgrass was selected. This area was subdivided into 100 blocks, each 5 feet square. The stem-count method was compared with other methods on a supplementary series of 100 individual plants.

In all methods and with both series (blocks and individual plants) a 1-inch subtraction was made to allow for that portion of the plant usually considered unavailable for grazing on sagebrush-wheatgrass spring-fall ranges. Thus, in the ocular-estimate-by-plot and the ocular-estimate-by-average-of-plants methods, the estimate was made of the percentage of removal above 1 inch. In the measurement method a 1-inch subtraction was made from heights both prior to and after grazing. In determining volume removal all plants were uniformly clipped to a 1-inch height. This uniform subtraction affects in no way the accuracy of the results, since it was applied to all methods except the stem-count. Neither does the fact that a 1-inch subtraction was made in the test signify that in actual practice a similar procedure must be followed. Any of the methods tested will work equally well if all herbage to the ground level is considered.

Removal was accomplished artificially, by clipping, every effort being made to simulate actual sheep-grazing habits. Plant portions removed were retained and weighed. After all data had been taken on a plot, the remaining herbage was clipped and weighed separately, the total yield being the sum of the two weights. Percentage removal as obtained by this modification of the volume-by-weight method was used as a base because it provided accurate percentage utilization for each individual block.

In clipping, variations in removal on adjacent blocks were made extreme in order to test the degree of association between each of the methods and the actual volume removed. Actual removal by volume varied from 5 to 75 percent of the yield of individual blocks on the 100-block series and from 5 to 100 percent on the 100-individual-plant series.

In conducting the study, three individual observers estimated and measured independently. This was done in an effort to determine, for each of the methods, the degree of error between the observations of different individuals. Moreover, before the study was initiated and during the time it was being conducted, no individual, in making estimates of utilization, used any check against actual volume removal. Two of the individuals (1 and 2) were experienced in the ocular estimation of percentage utilization, but during the preceding summer had not worked together. The third (3) had no previous experience in estimating or in measuring utilization but simply followed oral directions in formulating estimates and making measurements. Thus, each method was subjected to the personal error that might be expected with three individuals working on an area at the same time or in consecutive years.

Methods of obtaining percentage utilization were adapted to and used in the following manner for the experimental study: The measurement method was conducted on both the 100-plant and 100-block series. Average leaf measurements on all plants were made prior to and after simulated grazing by clipping. Using the average height before simulated grazing as 100 percent, the percentage utilization was calculated by comparing the two heights. The stem-count method, because it was found to be laborious, was confined to the 100-plant series. The ocular-estimate-by-plot method was conducted on the 100-plot series, estimates of each plot being made separately. Because the ocular-estimate-by-average-of-plants method was devised during the progress of the study, its test was confined to 20 of the 100 blocks.

STATISTICAL METHODS

Three statistical methods were used in the analysis of data. Similarity or dissimilarity between field methods on the 100-block and 100-plant series was studied by the standard error of the differences between means. Degree of association between percentages calculated by the various methods and actual volume removal was tested using correlation coefficients.

Since the data were in the form of paired observations, it was possible in determining standard errors of mean differences to use the formula

$$\sigma_{1-2}=\frac{\Sigma D^2-(\Sigma_D)(M_D)}{N^2}$$

in which σ is the standard error, D the difference between methods or individuals on the same plots, and N the number of plots. By this formula variability due to treatment is eliminated and the resultant standard error is due entirely either to the method or to the individual. Differences exceeding twice their standard error were considered significant.

Degree of association between actual removal and percentages derived by other methods was determined, using Ayres' commonly used formula for calculating a correlation coefficient (*2, p. 43*).

$$r_{xy}=\frac{\Sigma xy-\Sigma xMy}{\sqrt{\Sigma x^2-\Sigma x(Mx)}\ \sqrt{\Sigma y^2-\Sigma y(My)}}$$

Because two of the methods under study were for use with paired plots, paired transects, or paired series of randomized plots, data collected on yield were compiled and used to test the degree of dissimilarity existing on a limited area of this range.

Significance of differences between individuals was calculated from the summary tables using the formula (7) standard error of the difference between differences of individuals 1 and 2 from volume = $\sqrt{\sigma_1^2+\sigma_2^2}$.

RESULTS OF TESTS

ACCURACY AND PERSONAL ERROR

Since accuracy in methods that involve the use of an estimate is closely related to personal error, these two factors are dealt with simultaneously.

With data from the 20-block series comparisons were made between actual volume removed and measurement, ocular-estimate-by-average-of-plants, and ocular-estimate-by-plot methods. A statistical analysis of these data is presented in table 1.

TABLE 1.—*Comparison of data from ocular-estimate-by-plot, ocular-estimate-by-average-of-plants, and measurement methods*

[Data from 20 plots]

Method and estimator	Mean percent removal	Standard error of mean	Difference from volume	Standard error of difference	Ratio $\frac{D}{SE}$ [1]	Correlation with volume
Volume-by-weight (modified)	37.0	4.13				
Ocular-by-plot:						
Individual 1	40.8	5.50	3.75	2.66	1.4	0.8860
Individual 2	44.0	5.28	7.00	1.98	3.5	.9412
Individual 3	46.5	4.65	9.50	2.41	3.9	.8566
Ocular-by-average-of-plants:						
Individual 1	35.0	3.71	−2.05	1.49	1.4	.9335
Individual 2	39.9	3.94	2.85	1.66	1.7	.9166
Individual 3	38.1	3.85	1.05	1.68	.6	.9144
Measurement:						
Individual 1	41.6	2.99	4.65	2.12	2.2	.8714
Individual 2	35.2	4.13	−1.75	1.79	1.0	.9061
Individual 3	51.8	2.18	14.75	2.92	5.1	.7396

[1] $\frac{\text{Mean difference}}{\text{Standard error of difference}}$.

Using the standard error of the differences as a criterion, the average differences between percentage removal as obtained with the ocular-estimate-by-average-of-plants method and actual volume removed are but slight and insignificant for each individual observer. In contrast, percentage removal as indicated by the ocular-estimate-by-plot method differs appreciably from the actual removal, and this difference, in the case of individuals 2 and 3, is highly significant. Estimated percentage removal by measurement is very erratic between individuals, and when compared with actual volume removal, the figures of individuals 1 and 3 differ significantly.

Differences between individual estimates are indicative of the extent to which personal error is inherent in each method. When the ratio of the mean difference to its standard error is 2 or less the difference is insignificant statistically and personal error is regarded as low.

Ratios of the mean differences between individuals 1 and 2, 1 and 3, and 2 and 3 and their standard errors are calculated from figures presented in table 1. For ocular estimate by plot, the ratios of 1.0, 1.6, and 0.8 indicate a similarity in estimates between individuals. For ocular estimate by average of plants, ratios of 2.2, 1.4, and 0.8 show only the difference between individuals 1 and 2 to be significant. In contrast, ratios of 2.3, 2.8, and 4.8 show the personal error to be high in the measurement method.

Percentage removal determined by the stem-count method (table 2) tends to be uniformly greater than actual removal. Eighty-four of the one hundred percentages taken by this method had positive differences ranging as high as 73 percent above the actual removal. Its correlation with volume ($r=+0.7770$) indicates that this method is not definitely superior to measurement or to ocular estimates in association of estimates with actual removal, despite its simplicity and the reduction of personal error.

Data presented in table 2, in contrast to those in table 1, show a reversal in the reliability of the measurement and ocular-estimate-by-plot methods. Percentages obtained by all individuals using the ocular-estimate method differ significantly, whereas only that by individual 1 using the measurement system differs significantly from the actual volume. Higher correlations with actual volume were found for the measurement method than for ocular estimates.

Ratios of the mean differences to their standard errors calculated from data presented in table 2 are as follows: Between individuals 1 and 2, 1 and 3, and 2 and 3, using the measurement method, 2.4, 1.9, and 0.2; and using the ocular-estimate-by-plot method, 2.0, 2.4, and 0.2. In both methods the percentages recorded by individual 1 are significantly different from those recorded by 2 and 3.

TABLE 2.—*Comparison of data from ocular-estimate-by-plot, measurement, and stem-count methods on 100 individual plants*

Method and estimator	Mean percent removal	Standard error of mean	Difference from volume	Standard error of difference	Ratio $\frac{D}{SE}$ [1]	Correlation with volume
Volume-by-weight (modified)	53.77	2.38				
Stem-count	68.36	2.57	14.59	1.67	8.8	0.7770
Ocular-by-plot:						
Individual 1	44.40	2.30	−9.37	1.14	8.2	.6852
Individual 2	48.00	2.54	−5.77	1.36	4.2	.6777
Individual 3	48.35	2.36	−5.42	1.15	4.7	.8834
Measurement:						
Individual 1	47.26	2.14	−6.51	1.46	4.5	.7852
Individual 2	52.12	2.03	−1.66	1.38	1.2	.8831
Individual 3	51.58	1.86	−2.19	1.77	1.2	.8158

[1] $\frac{\text{Mean difference}}{\text{Standard error of difference}}$.

Analysis presented in table 3 shows the ocular-estimate system to be superior to the measurement system both in the slightly smaller average differences and in the higher correlations with actual volume removal.

Ratios of the mean difference between individuals 1 and 2, 1 and 3, and 2 and 3 and their standard errors are calculated from data presented in table 3. For the measurement method, ratios of 2.4, 7.2, and 9.0 show that all differences between individuals are large and

significant. For the ocular-estimate method, ratios of 1.4, 5.5, and 3.9 indicate that differences between individuals are small except for individual 3, whose estimates are significantly higher than those of individuals 1 and 2. This record, when compared to data from the 100-plant series in which the estimates of individual 1 were significantly lower than those of 2 and 3, shows that personal errors are not consistent from time to time. Since no discussion took place between individuals during the study, these inconsistencies show the necessity for frequent checking both between individuals and with actual volume removal.

TABLE 3.—*Comparison of data from ocular-estimate-by-plot and measurement methods on 100 25-square-foot blocks*

Method and estimator	Mean percent removal	Standard error of mean	Difference from volume	Standard error of difference	Ratio $\frac{D}{SE}$[1]	Correlation with volume
Volume-by-weight (modified)	33.97	2.75				
Ocular-by-plot:						
Individual 1	34.66	4.56	0.69	1.11	0.6	0.8645
Individual 2	36.86	4.91	2.89	1.13	2.6	.9032
Individual 3	42.39	4.04	8.42	.88	9.6	.9040
Measurement:						
Individual 1	37.23	2.77	3.26	.86	3.8	.8575
Individual 2	34.18	2.28	.18	.97	.2	.8315
Individual 3	47.09	1.32	13.12	1.06	12.4	.7740

[1] $\frac{\text{Mean difference}}{\text{Standard error of difference}}$.

RAPIDITY OF METHODS

Although detailed records were not kept of the time consumed in conducting each method, the ocular-estimate-by-plot method required the least. Field work and compilation required approximately 1 hour for 15 estimates by this method, whereas approximately 50 percent more time was needed for the same number of observations when the ocular-estimate-by-average-of-plants method was used. The volume-by-weight and the measurement methods each took two to three times as long and the stem-count method required from three to four times as long as the ocular-by-plot method.

EFFECT OF SOIL HETEROGENEITY AND DIFFERENCES IN INDIVIDUAL PLANT GROWTH

Since the measurement and the volume-by-weight methods of determining percentage utilization are designed primarily for use with paired plots or transects, or with two series of plots, errors in the use of these methods arising from soil heterogeneity and plant growth differences must be expected. In pairing individual plots or transects it is assumed that the two areas are similar in yield but, owing principally to variations in soils and plant growth, this assumption is seldom true. Although no extensive study of these two factors was attempted, some of the data collected definitely show a high dissimilarity to exist within a limited area.

Plots were so situated that 48 pairs could be obtained without duplication. Only contiguous plots were paired. The initial 48 pairs were divided by random selection into 2 groups of 24 pairs; 4

groups of 12 pairs, and 8 groups of 6 pairs (table 4). Mean yields of odd-numbered plots were chosen as a base from which the percentage deviation of the yield of even-numbered plots was computed.

TABLE 4.—*Difference in percent between series of paired plots based on deviation of relative yields*

48 paired plots	2 groups of 24 paired plots	4 groups of 12 paired plots	8 groups of 6 paired plots
−3.2	3.7	11.2	−0.6
	−7.9	−3.8	31.5
		−19.6	−3.5
		5.3	−2.1
			−16.2
			−10.8
			21.6
			−9.6

Using a 10-percent difference as the limit of accuracy, 2 series of 12 pairs and 4 series of 6 pairs were so different in yield, owing to soil heterogeneity and plant-growth differences, as to be of little use for the determination of percentage utilization. Differences between individual pairs were even more extreme, ranging from −61.3 percent to 175.4 percent. When high differences in yield occur in a limited area (25 by 100 feet) purposely selected because of apparent uniformity within the area, it is reasonable to expect a greater diversity over extensive areas.

Data from the 100-individual-plant series were studied as an indication of the degree of diversity of individual plant production. These data (table 5) were first segregated at random into 2 groups of 50 plants each, then further into 5 groups of 20 plants.

TABLE 5.—*Test of paired-plant series, yield data from 100 individual plants*

Series	Plants	Range in weight	Mean weight	Standard error of mean	Difference between series	
	Number	*Grams*	*Grams*		*Series*	*Percent*[1]
1	50	0.77–10.39	3.525		1–2	−11.5
2	50	.68–14.78	3.120		a–b	3.0
a	20	.85– 8.00	3.255	0.428	b–c	8.1
b	20	.68– 9.83	3.352	.564	c–d	−15.5
c	20	.85–14.78	3.622	.686	d–e	8.6
d	20	.71–10.39	3.062	.571	a–e	2.2
e	20	.77– 9.51	3.326	.580	b–e	−.8
					c–e	−8.2
					a–c	11.3
					a–d	−5.9
					b–d	−8.7

[1] Increase or decrease of the second-named series over the first.

Individual plant production differs widely, as is indicated by the range in yield of the individual plants, 0.68 to 14.78 g, and by differences in mean yields of paired 20- and 50-plant series as great as 15.5 and 11.5 percent, respectively. Thus, with two contiguous parallel plots, each containing approximately 50 plants, the dissimilarity in individual plants might introduce an error of 11.5 percent in percentage utilization.

These data, although not conclusive, serve to give an indication of the risk inherent in the use of an inadequate number of paired plots. Before either the measurement or volume-by-weight methods are used, a careful investigation should be made of the number of plots required to overcome the possible error because of soil heterogeneity and plant-growth differences.

DISCUSSION AND COMPARISON OF METHODS

Under actual grazing conditions, the volume-by-weight method requires the use of paired plots or paired transects. Since soil heterogeneity and plant-growth differences are frequently responsible for inaccurate results from individual paired plots or transects, variations in forage utilization on an area cannot be accurately measured by this method without plot or transect replication. In view of the labor required to secure adequate replication to overcome soil and plant differences or to picture variations in forage utilization the method as originally described is not desirable for use on range grasses. However, the volume-by-weight method, as modified in this study, can be used in the field to determine the degree of accuracy of any other methods being used.

As shown in tables 1, 2, and 3 the measurement method does not provide sufficient accuracy over the ocular-estimate method to serve as a check by which to determine the accuracy of other methods, and because of the increased labor involved in making observations and in compiling data it is not suited for extensive utilization studies. The measurement method also appears to be mechanically imperfect, because it presupposes that volume of grasses varies directly with average height. This supposition, together with the necessary ocular estimate of average height, may be accompanied by serious error. If several measurements are to be taken on each plant instead of one estimate of the average, the method becomes so tedious as to prohibit its use where numerous replications are necessary. Moreover, since the measurement method also necessitates the use of paired plots or transects, it is as difficult to use as the volume-by-weight method and subject to the same criticism.

As applied to bunch grasses, the stem-count method was the least accurate studied. Average errors are not of such great magnitude as those found by Pechanec (4) in studying the method on rootstock grasses, but they are, nevertheless, positive and cumulative. The stem-count method was found to be theoretically unsound since it is based upon the premise that the entire individual plant is removed by grazing. Since this degree of removal seldom occurs under actual conditions, errors are consistently positive. However, an estimate of the percentage of grazed stems removed, multiplied by the percentage of stem grazed, might yield more consistent results. The method is very laborious for use in the study of bunch grasses.

The ocular-estimate-by-plot method is reasonably accurate, sensitive to fluctuations in volume removal and rapid in operation. Since the method is subject to personal error, comparisons of data obtained by different individuals should be checked frequently with actual volume removed. Where possible, two or more individuals should be used to conduct observations during any one year in order that records in successive years will closely approximate each other. Estimates by this method, because they can be so rapidly made, permit a study of variations of grazing use on range units.

The ocular-estimate-by-average-of-plants method deserves consideration in long-time pasture and range studies. Its relative freedom from personal error and its high correlation with volume removal particularly adapt it to accurate range studies. As it is but slightly less rapid than the ocular-estimate-by-plot method, numerous replications can be made. Since the ocular-estimate-by-average-of-plants method is primarily designed for use with bunchgrasses or species that occur in definite clumps, it cannot be used without further adaptation on pastures or ranges where rootstock grasses are predominant.

FIELD USE OF THE OCULAR-ESTIMATE-BY-PLOT METHOD

On the range, presupposing that proper number, size, and distribution of plots have already been determined by appropriate tests designed for this purpose, the ocular-estimate-by-plot method of determining percentage utilization should be conducted in the following manner:

Each individual estimator should spend at least 1 day checking against determinations by the modified volume-by-weight method, as follows: Simulate grazing by clipping on plots of a limited size; retain the portions removed by clipping; and then make estimates of percentage removal on each plot. After completing estimates, remove the remainder of the herbage from the plot; weigh both lots of herbage; and determine the error of estimate by comparison with percentage removal calculated from the ratio of these two lots of herbage. By means of a progressive series of estimates and checks against actual percentage removal of weight, each estimator should be able to train himself to recognize accurately varying degrees of utilization. Where several men work together it is advantageous to have each individual simulate grazing on a different plot. Each individual then estimates percentage removal on his own plot and on those of the others as well. Thus many more checks are secured with the same amount of time and effort, and the objectionable feature of having known exactly the height and growth on each plot before simulated grazing is partially eliminated.

After each individual has trained in this manner, for each species that is to be estimated, the field crew is ready to begin work. In the field each estimator merely makes estimates of percentage removal by species on permanently or temporarily located plots. At regular intervals, the entire crew assemble and, using the modified weight method, check on a number of plots, preferably 10 each day. Then during the day any estimator, with the aid of a small spring scale, a paper sack, and a pair of scissors can check at will. All checks made during the day should be recorded. From these permanent records of the accuracy of each individual's estimates, the degree of accuracy of estimate for any area can be approximately determined.

Several very desirable features are combined in ocular-estimate methods where frequent reference is made to determinations by the modified volume-by-weight method.

(1) Ocular estimates by plot are reasonably accurate, and if frequent checks are made the degree of accuracy indicated by results of this study can be improved upon.

(2) Estimates can be made rapidly, facilitating abundant replication of plots.

(3) Estimates can be checked by comparison with percentages obtained by the modified volume-by-weight method. This is especially important since it furnishes as a base for comparison a percentage that is almost entirely free from personal error.

(4) Degree of accuracy of an average estimate for any area can readily be determined from an analysis of the record of checks.

(5) This method should be found widely adaptable to many different species, including grasses, weeds, and shrubs. It has been used on species falling in these groups since 1934 at the United States Sheep Experiment Station.

SUMMARY

A purely experimental study was conducted on the United States Sheep Experiment Station range near Dubois, Idaho, to test the limits of accuracy, the inherent personal error, and the rapidity of several methods of determining percentage utilization of range forage by grazing. The study was conducted on sagebrush-wheatgrass range on which bluebunch wheatgrass (*Agropyron spicatum*) and threetip sagebrush (*Artemisia tripartita*) were the principal species. One hundred plots, 5 feet square and arranged in a rectangle 25 by 100 feet, were used. Bluebunch wheatgrass, a bunchgrass species, was used in testing all methods.

Clipping to simulate removal by sheep was used as a substitute for grazing. This allowed the use of an accurate check in the form of the modified volume-by-weight method with which to compare other methods. Portions removed in the simulated grazing were retained and compared by weight with that left to determine the volume removal.

Utilization percentages were determined with the measurement and the ocular-estimate-by-plot methods on 100 blocks; by these methods and by the ocular-estimate-by-average-of-plants on 20 blocks; and by the stem-count, the measurement, and ocular-estimate method on 100 individual plants. Comparisons were made with percentages derived by the modified volume-by-weight method to test the accuracy of determinations by various methods.

The ocular-estimate-by-plot method may be very useful in range and pasture studies if a frequent check is maintained between individual estimators and with the actual percentage removal as determined with the modified volume-by-weight method. If these precautions are taken the method is particularly meritorious because of its rapidity of operation and its high correlation with actual volume removal. Furthermore, because of its rapidity of manipulation, numerous replications may be obtained. By this method estimates of percentage weight removal can be made on frequently replicated, randomized plots of a limited area. Percentage removal is estimated, for each species, on the plot as a whole.

The ocular-estimate-by-average-of-plants method is rapid, reduces personal error to an appreciable extent, is relatively accurate and is sensitive to fluctuations in actual utilization. From the data presented, this method is shown to be probably the most worthy of more study and development. It is the same as the ocular-estimate-by-plot method except that it is modified so individual estimates are made for each plant of the species being observed, the estimate for the plot being an average of these individual estimates.

The stem-count method is neither sufficiently accurate nor rapid to justify its use on bunchgrasses.

Owing to its lack of rapidity, the measurement method is not recommended for general use. It is not of sufficient accuracy to be used as a check on ocular estimates.

Because of the labor involved in individual determinations and the use of paired plots, the volume-by-weight method is not justifiable for use under actual range practices. However, as modified in this study, the method is valuable for use as a check on the accuracy of estimates by other methods.

From data and analyses presented it is recommended that ocular-estimate methods of obtaining percentage utilization, supplemented by comparison with determinations made by the modified volume-by-weight method, be considered for use in range pasture or open-range studies.

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VARIATIONS IN EGG-QUALITY CHARACTERS IN CERTAIN BREEDS, VARIETIES, AND STRAINS OF CHICKENS[1]

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INTRODUCTION

Recent trends in research in the field of egg quality have been toward the study of the initial condition of the egg rather than the changes that occur during holding periods under varying environmental influences. Most investigators have concerned themselves largely with the so-called interior egg-quality characters and more particularly with the albumen portions of the egg. Practically all such studies have been confined to single strains of a breed or variety with little or no evidence as to the comparability of different breeds, varieties, and strains.

Holst and Almquist (*4*)[3] demonstrated that percentage of firm albumen in the egg is a characteristic dependent on the individual hen. Lorenz, Taylor, and Almquist (*6*) gave further evidence of this and bred families of Single Comb White Leghorn that differed significantly with respect to this character. Van Wagenen and Hall (*11*) confirmed these findings and further showed that characteristic individual differences exist with regard to the score of the condition of the firm albumen, percentage apparent (outer) thin albumen, percentage inner thin albumen, yolk index, and yolk color.

Knox and Godfrey (*5*) found a significantly greater percentage of firm albumen in the eggs of the White Leghorn than in those of the Rhode Island Red, and suggested that such differences might be influenced by proper selection. Wilcke (*14*) observed that eggs from individual inbred hens were more uniform with respect to the combined viscosity of the entire contents of the egg than were eggs from noninbred birds.

Halnan and Day (*3*) concluded from a candling study of the eggs laid at the West Suffolk Egg Laying Trials during 1931–34 that there is no correlation between productivity of the bird and egg faults (meat spots, blood spots, watery whites, dropped yolks, and deformed shells). They also observed that the occurrence of a particular type of fault appears to be definitely linked with the individual bird rather than with external conditions, and has been shown to be associated more with certain strains than with others.

Since the egg-quality studies conducted at this station have been, in the main, with a single strain of birds, it was desired to secure

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[3] Reference is made by number (italic) to Literature Cited, p. 777.

comparisons with eggs from other strains and breeds of birds and to determine any variations that might exist in the characters of egg quality measured.

MATERIALS AND METHODS

Observations were made on the eggs of 1,273 individuals from 81 pens of Single Comb White Leghorn, 16 of Barred Plymouth Rock, 10 of White Plymouth Rock, 16 of Single Comb Rhode Island Red, and 10 of New Hampshire, managed and fed under practically uniform conditions, at the Central and Western New York Egg Laying Tests. The mean number of birds per pen was 9.6, with a range of from 5 to 13. These birds, bred and raised by many different poultrymen widely distributed geographically, were felt to be representative of production-bred flocks of their breeds.

Measurements of the quality characters of the 3,043 eggs were made by the authors at the two laying tests in May 1936. All eggs were examined the same day as laid, on 2 or 3 successive days in each of 2 weeks at each test, covering a period of 4 weeks in all.

Three measures of the quality of the albumen of the eggs were used in this study. The first of these was the score of the observed condition of the firm albumen. For this measure the condition of the albumen, as it appears when the egg is opened out on a flat surface, is scored by comparison with the photographic standards of Van Wagenen and Wilgus (*13*). These grade from the score 1.0, which represents an egg in which the firm albumen stands up well about the yolk and retains the egg shape, to score 5.0, in which no firm albumen is apparent.

The score of the condition of the firm albumen was supplemented by the height of the firm albumen measured in millimeters as described by Wilgus and Van Wagenen (*15*).

The third measure of albumen quality used was the percentage of firm albumen, a measure similar in nature to that described by Holst and Almquist (*4*) but determined in this instance by the Sharp pipette method of separation described by Van Wagenen and Wilgus (*12*).

Shell strength was measured by the weight, in kilograms, necessary to crack or crush the shell on a moving weight and lever device described by Romanoff (*8*).

As the eggs were opened, notations were made concerning the presence of common abnormalities. These consisted entirely of meat spots and blood spots. Any foreign bodies floating free in the albumen were designated meat spots, while matter that was obviously blood and generally in close proximity or adhering to the yolk surface was designated blood spots. These classifications were further subdivided by listing as small blood spots or small meat spots such of these abnormalities as were too small in size to be readily apparent in the normal candling procedure (approximately one-eighth of an inch or less in diameter).

Production was measured by the number of eggs laid and by the number of "points" earned according to the standard egg-laying-test scale of points during 30 weeks, or the period from the beginning of the test year to the midpoint of the period during which egg-quality observations were taken.

ANALYSIS OF DATA

Since previous work has shown that the quality characters used are relatively constant for an individual, variations due to unequal numbers of eggs laid by each hen during the test period have been eliminated in this analysis by taking the average of the eggs of each individual as a unit, except in the discussion of abnormalities. Where data from two eggs were in close agreement, the average of these was taken as the standard for that bird, but where data obtained from the first two eggs opened did not agree closely, further eggs were examined. In no case were more than four eggs necessary to obtain the average for a bird. The only observations that were discarded were those where only one egg was obtained from an individual or where measurements were lost or incomplete because of accident. The mean number of eggs opened per bird was 2.4.

For convenience in tabulation and analysis, the bird averages and attendant data were placed on cards for use in Hollerith machines. In addition to breed means with accompanying standard errors and standard deviations, correlation and analysis of variance studies were made.

The mean of each of the four quality characters and of production for each breed is shown in table 1, together with its standard error and standard deviation. The data for the Single Comb White Leghorn were analyzed separately for each test and serve as a basis for comparing all the data from the two tests. The only significant differences between the eggs of the groups of Single Comb White Leghorn at the two laying tests were with respect to percentage of firm albumen and shell strength. The Single Comb White Leghorn at both tests were combined in calculating the averages for this breed and all the birds of the five breeds and varieties were taken together to obtain the general average for all birds. A corrected mean for the five breeds is also shown.

TABLE 1.—*Means, standard errors, and standard deviations of four measures of egg quality and production for five breeds of chickens*

Breed	New York laying test	Birds	Score of condition of firm albumen [1]			Height of firm albumen			Percentage firm albumen		
			Mean	S. E.	S. D.	Mean	S. E.	S. D.	Mean	S. E.	S. D.
		Number				*Millimeters*	*Millimeters*	*Millimeters*	*Percent*	*Percent*	*Percent*
Single Comb White Leghorn	Central	370	1.99	±0.026	±0.512	6.45	±0.068	±1.30	62.5	±0.281	±5.40
Do	Western	390	2.03	.028	.546	6.44	.068	1.34	64.5	.308	6.09
Do	Both	760	2.01	.019	.530	6.45	.048	1.32	63.5	.212	5.84
Barred Plymouth Rock	Central	160	2.22	.052	.652	5.79	.116	1.47	66.9	.497	6.28
White Plymouth Rock	do	94	2.14	.059	.573	6.07	.145	1.41	66.3	.619	6.00
Single Comb Rhode Island Red	Western	157	1.99	.043	.539	6.53	.103	1.29	66.2	.456	5.72
New Hampshire	do	102	1.98	.055	.556	6.61	.144	1.45	64.6	.520	5.26
All birds		1,273	2.04	.016	.560	6.36	.039	1.38	64.5	.168	6.01
5 breeds			2.06			6.29			65.5		

Breed	New York laying test	Birds	Shell strength			Eggs laid			Production points [2]		
			Mean	S. E.	S. D.	Mean	S. E.	S. D.	Mean	S. E.	S. D.
		Number	*Kilograms*	*Kilograms*	*Kilograms*	*Number*	*Number*	*Number*			
Single Comb White Leghorn	Central	370	4.14	±0.054	±1.03	136.6	±1.35	±25.9	138.3	±1.42	±27.2
Do	Western	390	3.89	.051	1.01	139.9	1.47	29.0	143.3	1.53	30.2
Do	Both	760	4.01	.037	1.03	138.3	1.00	27.6	140.8	1.05	28.9
Barred Plymouth Rock	Central	160	3.77	.072	.91	136.7	2.58	32.7	135.9	2.60	32.8
White Plymouth Rock	do	94	3.95	.093	.91	131.6	2.43	23.5	133.1	2.49	24.1
Single Comb Rhode Island Red	Western	157	3.93	.087	1.09	138.8	2.14	26.8	141.8	2.31	29.0
New Hampshire	do	102	4.06	.085	.86	137.3	2.70	27.3	141.7	2.82	28.4
All birds		1,273	3.97	.028	1.01	137.6	.78	27.9	139.8	.81	29.2
5 breeds			3.95			136.5			138.7		

[1] Score 1.0=Firm albumen and 5.0 no apparent firm albumen.

[2] On standard egg-laying test scale.

SCORE OF THE CONDITION OF THE FIRM ALBUMEN

No differences with respect to the score for the condition of the firm albumen were found among the Single Comb White Leghorn, Single Comb Rhode Island Red, or New Hampshire as breeds, nor was the difference between the White Plymouth Rock and the Barred Plymouth Rock significant. However, mathematically significant differences existed between each variety of Plymouth Rock and any of the three other breeds, the eggs from the Plymouth Rock breeds showing a poorer condition of the firm albumen than those of the Single Comb White Leghorn, Single Comb Rhode Island Red, or New Hampshire.

TABLE 2.—*Analysis of variance of score for condition of firm albumen of the eggs of individuals, pens, and breeds*

Correlation and breed	New York laying test	Sums of squares	Degrees of freedom	Mean square	Ratio	Odds
Breeds and within breeds:						
American breeds	Both	Total 3.2258	51	0.2314	4.38	>99:1
		Breeds .6943	3	.0527		
		Remainder 2.5315	48			
All breeds	do	Total 6.7883	93			
		Breeds .7595	4	.1899	2.803	>19:1
		Remainder 6.0288	89	.06774		
Pens and within pens:						
Single Comb White Leghorn.	Central	Total 116.4559	389			
		Pens 27.4490	41	.66948	2.62	>99:1
		Remainder 89.0069	348	.25577		
Single Comb White Leghorn.	Western	Total 96.8391	369			
		Pens 20.5306	38	.54028	2.34	>99:1
		Remainder 76.3085	331	.23054		
Barred Plymouth Rock	Central	Total 68.0001	159			
		Pens 5.9068	15	.3938	.91	<19:1
		Remainder 62.0933	144	.4312		
White Plymouth Rock	Central	Total 30.8121	93			
		Pens 2.7098	9	.30111	.90	<19:1
		Remainder 28.1023	84	.3346		
Single Comb Rhode Island Red.	Western	Total 45.6420	156			
		Pens 4.8150	15	.3210	1.11	<19:1
		Remainder 40.8270	141	.2895		
New Hampshire	Western	Total 28.2040	101			
		Pens 4.3158	9	.4795	1.85	<19:1
		Remainder 23.8882	92	.2597		
All breeds	Both	Total 398.5648	1,272			
		Pens 74.9656	132	.56792	2.00	>99:1
		Remainder 323.5992	1,140	.28385		

Analysis of variance (*2*), presented in table 2, showed that there was significantly greater variation between breeds than within breeds as measured by Snedecor's (*9*) value of F. On the other hand, the same statistic showed that there was significantly greater variation between pens than within pens for the entire group of birds, but a more detailed analysis by breeds showed this to be true only within the two relatively larger groups of Single Comb White Leghorn. Thus in the breeds of the American class studied, there was greater variability with regard to the condition of the firm albumen among the eggs of individuals within a pen or strain than between the pens, whereas in the Single Comb White Leghorn the variation was greater between pens than within pens, the difference being of high significance mathematically. Larger numbers of birds might possibly have increased the significance of the variation found in the heavier breeds, but there can be no question that the American breeds, as a whole, were much less uniform within pens than was the Single Comb White Leghorn breed. If the birds at these two laying tests can be taken

as representative of their breeds, it may be assumed that the more widespread and intensive breeding operations with the Single Comb White Leghorn have tended to produce a greater uniformity within strains as regards the condition of the firm albumen in the eggs than is true with the four other breeds studied. These differences among breeds confirm previous observations of the authors. Nevertheless, it may not be implied that they are universal.

HEIGHT OF FIRM ALBUMEN

The close relationship of height to the score for the condition of the firm albumen as pointed out by Botsford (*1*) and by Wilgus and Van Wagenen (*15*) is further substantiated by the correlations between these two measures shown in table 5. Therefore, it is reasonable to expect the same variations with regard to this character as were pointed out for the condition of the firm albumen. The statistical analysis proved this reasoning valid, and the same conclusions may be drawn here as were before stated.

PERCENTAGE FIRM ALBUMEN

As previously mentioned, eggs of the Single Comb White Leghorn at the western test had a higher percentage of firm albumen than did those of the same breed at the central test (table 1). This difference of 1.97 percent was not large and probably has little practical importance in spite of its mathematical significance. A frequency distribution of the pens at the two tests showed a few pens with an exceptionally high percentage of firm albumen at the western test. This accounted for most of the differences between the two groups. The analysis of variance for this factor (table 3) showed that there was greater variation between pens than within pens, which is suggestive of strain differences.

TABLE 3.—*Analysis of variance of the percentage firm albumen of the eggs of individuals, pens, and breeds*

Correlation and breed	New York laying test	Sum of squares		Degrees of freedom	Mean square	Ratio	Odds
Breeds and within breeds:							
American breeds	Both	Total	411.51	51			
		Breeds	28.66	3	9.553	1.198	<19:1
		Remainder	328.85	48	7.976		
Single Comb White Leghorn	do	Total	603.36	80			
		Breeds	80.89	1	80.890	12.23	>99:1
		Remainder	522.47	79	6.613		
All breeds	do	Total	1,229.05	132			
		Breeds	242.84	4	60.710	7.88	>99:1
		Remainder	986.21	128	7.705		
Pens and within pens:							
Single Comb White Leghorn	Central	Total	10,768.23	369			
		Pens	2,129.40	38	57.707	2.21	>99:1
		Remainder	8,638.83	331	26.099		
Do	Western	Total	14,425.84	389			
		Pens	3,689.14	41	89.979	2.92	>99:1
		Remainder	10,736.70	348	30.853		

The Single Comb Rhode Island Red and the two varieties of Plymouth Rock did not differ significantly among themselves with respect to the percentage of firm albumen. These three breeds laid eggs which average a slightly larger proportion of firm albumen than the eggs of the Single Comb White Leghorn and New Hampshire. The

Single Comb White Leghorn and the New Hampshire did not differ significantly. Analysis of variance of the data (table 3) from the four American breeds indicated that the variation within the breeds was greater than the variation between breeds. However, with all data included, the variation between breeds is greater than that within breeds because of the large numbers of less variable Single Comb White Leghorn. The higher proportion of firm albumen in the eggs of the Single Comb Rhode Island Red than in the Single Comb White Leghorn is not in agreement with the findings of Knox and Godfrey (*5*), who reported the opposite relationship. Nevertheless, it confirms their hypothesis that differences found are not unalterable. This hypothesis is further supported by the differences between the Single Comb White Leghorn groups at the two tests. These, together with the small gross differences between breeds, suggests that, while mathematical significance has been imparted to the observations by the numbers of individuals involved, it is doubtful whether biological importance can be safely implied.

SHELL STRENGTH

The strength of shell, expressed in kilograms necessary to crush or crack the egg, is also shown for each breed in table 1. The shells of the eggs of the Single Comb White Leghorn at the central test had a significantly higher breaking point than those at the western test. This indication of the relative shell strength at the two tests increases the significance of the low breaking point indicated by the Barred Plymouth Rock, which was the only group to differ significantly from the others of the breeds tested. This supports the findings as regards strength of shell in eggs reported by Taylor and Martin (*10*) and Morgan (*7*) for Barred Plymouth Rock and Single Comb White Leghorn. The great variability of the data on this character renders any practical implications of these differences of doubtful importance, with the exception of the one instance cited.

ABNORMALITIES

The blood and meat spots observed in the eggs opened are listed in table 4. For all birds and for each breed the total number of eggs opened is shown, together with the average number of eggs opened per hen and the percentage of each type of abnormality found. The striking observation from these data is found in the large proportion of eggs from the American breeds that contained meat spots. On the first day that the observations were made at the central test the meat spots were not subclassified on the basis of size. Thus, at the central test, small meat spots appear to be less frequent and meat spots more frequent than at the western test, but this difference is due to the method of classification. There can be no question but that there is a breed difference with respect to this abnormality. White eggs from the Single Comb White Leghorn contained only one-fourth as many meat spots as did brown eggs from the American breeds. While it is true that approximately one-half of the meat spots found were small enough not to be readily detectable before the candle, and, therefore, of little commercial importance, the number of large meat spots was great enough to represent a problem of real economic importance.

TABLE 4.—*Percentage of eggs from five breeds of chickens, showing meat spots and blood spots*

Breed	New York laying test	Eggs opened		Small meat spots	Meat spots	All meat spots	Small blood spots	Blood spots	All blood spots
		Total	Mean [1]						
		No.	*No.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*
Single Comb White Leghorn	Central	893	2.4	3.4	5.9	9.4	4.6	3.0	7.6
Do	Western	923	2.4	9.6	4.2	13.8	5.3	3.1	8.4
Do	Both	1,816	2.4	6.6	5.1	11.7	5.0	3.1	8.1
Barred Plymouth Rock	Central	395	2.5	11.6	24.6	36.2	4.8	4.1	8.9
White Plymouth Rock	do	220	2.3	9.5	30.5	40.0	4.5	4.1	8.6
Single Comb Rhode Island Red	Western	370	2.7	22.7	21.6	44.3	7.0	2.4	9.4
New Hampshire	do	242	2.4	25.2	23.1	48.3	5.0	3.7	8.7
All birds		3,043	2.4	10.9	12.9	23.8	5.2	3.2	8.4

[1] Average per hen.

Approximately the same occurrence of blood spots was observed in all the breeds. The percentage of both these abnormalities was considerably higher than that usually reported by candling establishments, but it must be recalled that the eggs were opened shortly after they were laid, and that, therefore, little time had elapsed in which dissolution of these spots, particularly the blood spots, might take place. Also the possibilities that the "spots" were undetectable in candling because of the chalazae, or a cloudy or particularly firm albumen or dark-colored yolk, were eliminated. The proportion of these abnormalities found in the eggs from the Single Comb White Leghorn closely approximates similar observations by the authors on over 5,000 eggs from the Cornell Experiment Station flock of Single Comb White Leghorn.

CORRELATIONS

Gross correlations were calculated between all possible pairs of characters for each breed and for the group as a whole. These are presented in table 5. Mathematically significant correlations were found in several instances between the condition of the firm albumen and the percentage firm albumen. The correlation between these characters was skewed by the inclusion of eggs in which the firm albumen envelope was ruptured, and is therefore invalid. A similar occurrence has been previously pointed out by Van Wagenen and Wilgus (*13*).

There was no correlation between the condition of the firm albumen and strength of shell. Nor was there any correlation between the percentage firm albumen and shell strength. In comparing production and shell strength a few of the coefficients of correlation were mathematically significant though the values of r were generally low.

Within the White Plymouth Rock and the New Hampshire breeds statistically significant correlation coefficients were obtained between condition of the firm albumen and production, but for the other breeds the coefficients for this association were not significant. These significant correlations, added to the fact that all coefficients are of the same polarity, might tend to support the theory that egg production is a factor in the lowering of egg quality as here measured. But the analysis of variance of the condition of firm albumen showed the

TABLE 5.—*Intercorrelations of several measures of egg quality and production within five breeds of chickens*

Breed	New York laying test	Between condition and percentage of firm albumen	Between height and percentage of firm albumen	Between condition of firm albumen and shell strength	Between percentage of firm albumen and shell strength
Single Comb White Leghorn	Central	−0.134 ±0.051	0.108 ±0.051	−0.016 ±0.052	−0.114 ±0.051
Do	Western	−.214 ±.048	.177 ±.049	−.022 ±.051	−.039 ±.051
Do	Both	−.171 ±.035	.144 ±.036	−.019 ±.036	−.093 ±.036
Barred Plymouth Rock	Central	−.266 ±.073	.251 ±.074	−.013 ±.079	+.112 ±.078
White Plymouth Rock	do	−.197 ±.105	.091 ±.102	−.026 ±.103	+.143 ±.101
Single Comb Rhode Island Red	Western	−.195 ±.077	.130 ±.078	−.008 ±.080	+.151 ±.078
New Hampshire	do	−.054 ±.099	.117 ±.098	−.018 ±.099	−.101 ±.098
All birds		−.151 ±.027	.119 ±.028	−.018 ±.028	−.034 ±.028

Breed	New York laying test	Between condition of firm albumen and production of eggs	Between height of albumen and production of eggs	Between percentage of firm albumen and production of eggs	Between shell strength and production of eggs	Between score for condition and height of firm albumen
Single Comb White Leghorn	Central	0.074 ±0.052	−0.096 ±0.051	+0.060 ±0.052	−0.190 ±0.050	−0.945 ±0.006
Do	Western	.086 ±.050	−.151 ±.049	−.109 ±.050	−.107 ±.050	−.949 ±.005
Do	Both	.082 ±.036	−.126 ±.036	−.026 ±.036	−.151 ±.035	−.946 ±.004
Barred Plymouth Rock	Central	.148 ±.077	−.153 ±.077	+.187 ±.076	−.244 ±.074	−.950 ±.008
White Plymouth Rock	do	.323 ±.092	−.393 ±.087	+.154 ±.101	−.227 ±.098	−.931 ±.014
Single Comb Rhode Island Red	Western	.124 ±.079	−.144 ±.078	−.237 ±.075	−.071 ±.079	−.937 ±.010
New Hampshire	do	.364 ±.086	−.417 ±.082	−.093 ±.098	−.170 ±.096	−.933 ±.013
All birds		.129 ±.028	−.164 ±.027	−.017 ±.028	−.155 ±.027	−.944 ±.003

heavy breeds to be highly variable within pens as compared to the less variable Single Comb White Leghorn. This, together with the smaller numbers involved, might also through chance explain these relationships which are believed to be of little practical significance. Partial correlation analysis with the characters available failed to change materially the value of r.

Percentage firm albumen and production were unrelated, the coefficients varying widely in value and direction among the various breeds, but in no case was it of any real significance.

In general, the correlation analysis supports the contention that the measures of egg quality used are independent of each other and of production, with the exception of the obvious relationship between the height and the score of the condition of the firm albumen. These two measures, as they are now used at this station, are closely associated and used as checks against each other. The simple correlation coefficient of -0.944 ± 0.003 between the height and the score of condition of the firm albumen is practically the same as that shown by Wilgus and Van Wagenen (*15*), on a much smaller group of eggs of all degrees of quality. The relationship was unchanged within any of the breeds, offering further evidence of the general applicability of these measures.

SUMMARY AND CONCLUSIONS

The eggs of the Barred and the White Plymouth Rock showed significantly poorer condition of the firm albumen than did the eggs of the Single Comb White Leghorn, Single Comb Rhode Island Red, and New Hampshire at the central and western New York egg-laying tests.

The Single Comb White Leghorn showed greater variability between pens than within pens, indicating strain differences for the condition and percentage of firm albumen. The American breeds did not show greater variability between pens than within pens.

The percentage of firm albumen and shell strength did not differ importantly among the breeds with the exception of the Barred Plymouth Rock, which showed slightly weaker shell strength.

Eggs from the American breeds studied showed a much greater incidence of meat spots than did those from the Single Comb White Leghorn. No differences in the occurrence of blood spots were observed among the breeds.

With the exception of the association between the height and the score of the condition of the firm albumen, none of the egg quality characters studied showed biologically significant interrelation with each other or with production, although mathematically significant association existed in some instances.

These data confirm previous observations by the authors that, for the most part, the characters used as measures of interior egg quality are independent of each other and are relatively constant for the individual.

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THE BIOLOGY OF MICROTINE CYCLES[1]

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INTRODUCTION

Striking increases in rodent populations have been recorded since Biblical times. Such plagues and the resultant economic losses have engaged the attention of scientists for years. More recently, and from the viewpoint of economic zoology, attention has been directed to these phenomena of cycles with their resultant change of population levels. Mass increases in a species are obvious, and have excited the interest of biologists periodically, so that an extended literature has resulted. Periods of scarcity of any species are far less noticeable, and accordingly are seldom recorded.

Microtine (short-tailed field mice or voles) species exhibit a regular periodicity in their cyclic behavior. A study of this subject is justified because of the damage to agriculture caused by these animals, particularly at the height of the cycle. By their destruction of fruit trees, hays, cereals, and garden truck, the annual loss runs into millions of dollars. A careful study of a cycle might well elucidate the factors responsible for the plague, and, if it does not suggest remedial measures, it might at least indicate some possibility of forecasting periods of optimum density. Thence practical control measures for the anticipated hordes of mice can be inaugurated.

REVIEW OF LITERATURE

Few detailed observations of cycles have been recorded. Lantz (*4*)[3] records a number of instances which clearly show the cyclic tendency of *Microtus*, but apparently was not cognizant of fluctuating populations and their periodic recurrence. Elton (*2*) and Middleton (*5*) observed vole cycles in Great Britain, Collett in Norway, mentioned by Elton and his coworkers (*2*), while recent studies in the Union of Soviet Socialist Republics by Vinogradov (*12*), Pidoplichka, according to Vinogradov, and Plater-Plochotzkij (*7*) suggest a cyclic tendency among microtines.

PERIODICITY OF CYCLES

All available evidence points to a 4-year cycle. Lantz (*4*) presents considerable data, gleaned from circulars distributed to orchardists, that *Microtus* was abnormally abundant in 1863, 1883, and 1887. During the summer of 1888 mice were notably scarce, following 2 years of abundance. Their numbers were again high in Ohio in 1890. Mice were extraordinarily abundant in 1903 and once more, after a notable

[1] Received for publication Dec. 14, 1936; issued June 1937.
[2] The writer is indebted to Dwight Soliberger for assistance in the collection of experimental animals during 1935 and 1936.
[3] Reference is made by number (italic) to Literature Cited, p. 789.

decrease, became abundant in the spring of 1906. One correspondent wrote of "remembering four to five seasons out of the past twenty-five when the pest was very, very numerous. It seems almost incredible how all of a sudden they come and then seemingly disappear."

Elton and his coworkers (*2*) and Middleton (*5*) give much evidence of the existence of a 4-year cycle in British voles. In Norway, Collett, according to Elton et al., presents data suggestive of a 3½-year cycle for *Microtus agrestis*. Vinogradov (*12*) has attempted to establish a 10-year cycle in the Union of Soviet Socialist Republics, these outbreaks occurring in the year ended with a 3 (i.e. 1763, 1933). His data, chiefly of a historical report, and not based on field work, rather suggest a much shorter period. Pidoplichka, as reported by Vinogradov (*12*), disputes a 10-year cycle in Russian voles, and shows that a maxima can be reached in 2½ years. Plater-Plochotzkij (*7*) indicates a short cycle for *M. pelliceus*, possibly of 3 or 4 years.

The investigators of Great Britain and the Union of Soviet Socialist Republics thus postulate a cycle in voles approximating 4 years. These data favor studies of the writer, which indicate a similar periodicity in northeastern United States. While the peak of a cycle usually terminates at the end of 4 years, increasing populations is not of necessity a gradual one. Under ideal conditions mice may reach plague proportions in 3 years. Similarly, populations at the peak of a cycle may not assume alarming proportions and do not always cause widespread destruction.

Extensive trapping records, quadrat studies, close field observations, and the records of county agricultural agents indicate that mice were extremely abundant in New York State during the winters of 1919–20, 1923–24, 1927–28, 1931–32, and 1935–36. G. C. Oderkirk, district agent of the United States Bureau of Biological Survey, writes (in litteris June 26, 1936) that in Illinois and Indiana population highs occurred in the general periods 1923–24, 1927–28, and 1931–32. Oderkirk further observed that mice were again very abundant in this area during the winter of 1935–36.

METHODS

The studies here recorded are based chiefly on field and laboratory observations on the field mouse (*Microtus pennsylvanicus pennsylvanicus* (Ord.)) in the Ithaca, N. Y., locality. Field notes are available from 1924 to 1936, but most of the data are based on intensive studies extending from the spring of 1933 until the fall of 1936. A total of 4,000 animals were examined, equally divided as to sex, and representing all ages. The distribution of the collections by months was sufficient to give reliable data.

In 1932 11 areas more or less defined by natural boundaries, were mapped. These areas, all supporting a microtine population, varied from one-half acre to 12 acres. Trapping was commenced in 1932, with snapback traps which were replaced in 1933 largely by traps designed to take the animals alive. From the spring of 1934 to the fall of 1936, trapping was conducted in every month.

In the larger areas, where snapback traps were placed, trapping was conducted for a week with 100 traps. The traps were all baited with oatmeal flakes (the most attractive of many baits tried). An area is thus quickly rendered free of mice, more than four-fifths of them

being trapped in the first 2 days. Unpublished data of the writer usually indicate that the home range of *Microtus* is very small, usually encompassing an area not exceeding 2,000 square feet. Thus trapping in the center of a 10-acre tract (while not depleting the population excepting in the middle of the area) will give a fair index to the population level for different years. Traps set at 10-pace intervals through the area (such stations being marked with permanent stakes) is another method which has proven satisfactory. Traps are set within 1 or 2 feet of the stakes and are thus easily recovered.

In areas up to 3 acres the mice caught alive were counted, marked, and released after the area had been trapped a week. This method, conducted similarly over a 4-year period, indicates roughly the fluctuations in the mouse population for the different areas under observation. Obviously some of the areas were better suited to mice than others and accordingly supported a larger population. All that were continuously studied for 3 or more years show a marked increase in mice from the fall of 1932 to the spring of 1936.

MOUSE POPULATIONS

Microtine numbers vary in any one locality from year to year. When at their peak, the voles frequently exist in incredible numbers; shortly after periodic decline few may be found. Piper (*6*) estimated 8,000 to 12,000 mice per acre during the Nevada plague of 1907. The fields were riddled with their holes, which were scarcely a step apart. Pidoplichka recorded few mice in an area of the Union of Soviet Socialist Republics in 1925; by 1927 their numbers had reached 6,000 per hectare. Fortunately, the eastern United States has never experienced such hordes, but the rise and fall of murine populations is none the less apparent to one who follows these from year to year. Townsend (*11*) estimated the population of *Microtus* in Central New York as 2 to 67 per acre in various habitats. From his studies, he believed *Microtus* was more abundant in 1933 than in 1934.

Estimates of population per acre based on trapping records over a 4-year period are indicated in figure 1. To substantiate these estimates, several areas were selected and thoroughly trapped. The populations actually existing in such areas agree essentially with the estimates based on a week of trapping.

Studies indicate a mouse population in the spring of 1933 ranging from 15 to 40 per acre depending on the habitat. Other factors being equal, larger areas produced higher populations per unit area than did the smaller areas. A gradual increase in the population occurred, with losses during the winters when no breeding was apparent. This increase culminated in apparent optimum densities of mice in the winter of 1935–36. Populations of 160 to 230 mice per acre were reached. At Ticonderoga, Essex County, N. Y., Lyle W. Johnson saw from 2 to 8 mice about each tree in his orchard during late November. Later, while removing mulch, he saw 3 to 4 mice per tree and estimated the mouse population during early December as 200 to 300 mice per acre. These populations are similar to those observed by Elton et al. (*2*), who indicate that voles reached densities of over 100 per acre, but probably less than 200 per acre on the Scottish border during the spring of 1934.

Population density of voles may be indicated by amount of fresh dung over unit areas. The droppings are characteristically green when fresh, and are usually deposited in little piles at irregular intervals along the runways. Less often they are scattered promiscuously

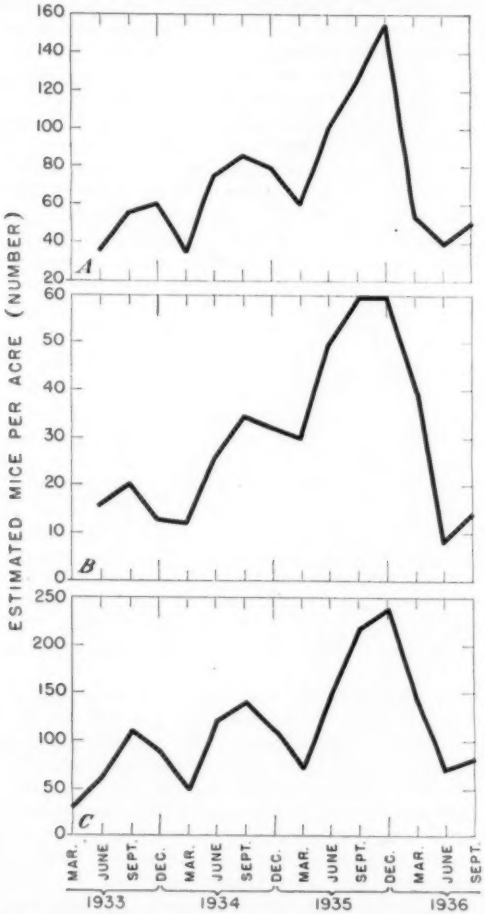

FIGURE 1.—Estimates of microtine population per acre based on trapping records over a 4-year period: *A*, area M, an 8-acre field supporting a heavy, mature stand of alfalfa which was never cut, and old stalks forming an ideal winter cover, with some *Crataegus* and a few small elms present; *B*, area F, a 6-acre field with no trees or shrubs, through the center of which runs a stream, the ground cover being chiefly *Festuca ocina* and orchard grass, forming a dense mat of excellent cover throughout the year; *C*, area A, a 20-acre orchard containing 3,500 young apple trees, the ground cover being principally alfalfa, red clover, quackgrass, and orchard grass, there being an excellent cover of dead grass.

along the trails. If suitable areas of sufficient size (3 to 10 acres) be selected, and counts of pellet middens be made in a uniform manner at regular intervals, some index to periodicity in population levels will be available. Spacing the counts at 10- or 20-foot intervals will eliminate the unconscious choice of likely stations.

A wire circle 20 inches in diameter was dropped at 20-foot intervals, 100 counts being made for each investigated area. Monthly records thus secured substantiated the trapping records and indicate a sharp decrease in mouse numbers in many areas from the winter of 1935–36 to the summer of 1936 (table 1).

TABLE 1.—*Fecal counts as an indicator of mouse abundance in a 12-acre field at Ithaca, N. Y.*

[Percentage of 100 stations showing fresh droppings at time indicated]

Date	Percentage of stations with fresh droppings	Date	Percentage of stations with fresh droppings	Date	Percentage of stations with fresh droppings	Date	Percentage of stations with fresh droppings
1934		*1934*—Con.		*1935*—Con.		*1936*	
March	24	November	65	May	92	March[1]	89
April	30	December	45	June	84	April	69
May	21	*1935*		July	78	May	21
June	43			September	91	June	23
July	40			October	83	July	29
August	33	January	62	November	98	August	16
September	58	February	55	December	94	September	27
October	69	April	86			October	31

[1] At 80 stations.

FACTORS RESPONSIBLE FOR CYCLIC INCREASE

Both biotic and abiotic factors contribute toward population oscillations. Among the biotic factors which permit increasing populations of small rodents might be mentioned a dearth of predators, parasites, and disease. Abiotic conditions favoring increase are physical and are mainly concerned with favorable climatic conditions such as mild winters or those with much snow, and wet summers. Rigorous winters with little snow and dry summers are reflected in a reduced population.

Obviously any change in the reproductive behavior of a species that would tend toward increased populations should be indicated during the waxing of a cycle. Actually, population densities are augmented by acceleration of the breeding rate, increased number of young per litter, and prolongation of the breeding season.

ACCELERATION OF THE BREEDING RATE

Microtine rodents are the most prolific breeders of all mammals. Their litters follow one upon another in rapid succession. Bailey (*1*) reared 13 litters from a single female *Microtus* within a year, while the writer had one female that produced nine litters in 8 months It is not known how long the mice stay in heat, but observations on captives indicate that the period is extremely short, perhaps a few hours. The oestrous period normally follows parturition. Fruitful copulation is thus possible immediately after the young are born. It is not uncommon to collect gravid nursing individuals. Repeatedly females are trapped that give evidence of very recent parturition, a bloody discharge being yet apparent. Ostensibly these promiscuous individuals are ready and willing to accept a male. Frequently a copulation plug is present when the uteri are yet distended following

partus. It thus seems apparent, from field observations, that one mating follows another in rapid succession when the two sexes are abundant enough to make this condition possible.

During periods of low population densities, the chances are greatly lessened of a female in oestrous meeting a fertile male. Such females might repeatedly pass the critical oestrous period before a successful mating occurs. This would lessen the rate of breeding.

Long familiarity with the appearance of breeding mice has enabled the writer to determine, from wild-caught specimens, whether or not they were lactating, and, if lactating, the approximate age of the nursing young. It was thus possible to determine, in pregnant individuals, by an examination of the teats, whether they were or were not nursing. If a high percentage of the nursing mice were gravid, it would indicate young were being produced exceptionally fast. If, on the other hand, few lactating mice were pregnant, it would appear that young were not being produced at an excessive rate.

Table 2 indicates the acceleration in the breeding rate from the fall of 1933 until the summer of 1936. It will be noted that during the period of mortality (March to June 1936) breeding was not materially affected, only a decrease in litter size being apparent. This is in contrast to the observation of Preble (*8*) who found during an epidemic among snowshoe rabbits a great curtailment in the breeding activities in the Athabasca-MacKenzie region in 1905. Local epidemics in widely scattered areas of New York (Westchester, Seneca, and Tompkins Counties) occurred from late March into the early summer of 1936.

TABLE 2.—*Percentage of nursing mice that were gravid as an index to the rate of breeding*

Month	Number of nursing mice examined and percent gravid in—							
	1933		1934		1935		1936	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
January			0	0	0	0	7	0
February			0	0	0	0	5	0
March			0	0	0	0	6	16.7
April			20	15.0	22	13.6	46	39.1
May			8	37.5	15	60.0	36	77.8
June			15	73.3	24	83.3	52	67.3
July			7	71.4	19	73.7	39	56.4
August			28	75.0	38	78.9	31	58.1
September	21	38.1	14	42.8	26	61.5	27	48.1
October	16	37.5	10	20.0	15	46.7	30	73.3
November	3	0	5	0	31	35.5	3	0
December	0	0	0	0	33	27.3		

INCREASED NUMBER OF YOUNG PER LITTER

Larger litters during the ascendancy of the cycle augment the mouse population. The number of young per litter ranges from 1 to 11. The average number, based on data from females taken in every month of the year, and over a 4-year period (1933–36), is 5.07. Embryo counts of necessity do not give an exact criteria of the young produced. Resorption of embryos frequently occurs, especially in the period approaching the peak of the cycle, or at its culmination. Young are occasionally still-born in captivity, and

this undoubtedly occurs also in the wild state. Yet sufficient embryo counts made over a period of years do indicate whether the number per litter is increasing or decreasing. Increased litter size was apparent in each of the corresponding months from 1933 until 1935 (fig. 2). With mice dying, probably from an epizootic, during the

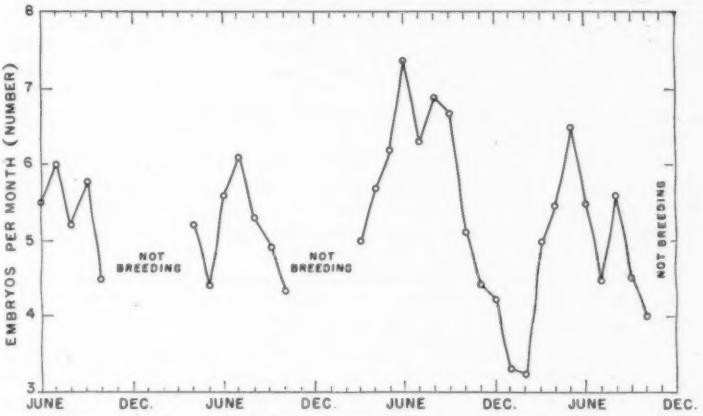

FIGURE 2.—Litter size for mice, as determined by embryo counts, from 1933 to 1936. The decrease of the mouse population during the spring of 1936 was accompanied by a decrease in litter size, the litters approximating those of 1933 and 1934 in size.

spring of 1936, a decrease in litter size followed. Thus the average number of embryos for July 1936 was 4.5, the corresponding month in 1933, 1934, and 1935 it was 6, 6, and 6.2, respectively.

PROLONGATION OF THE BREEDING SEASON

The breeding season of cyclic rodents varies from year to year, depending largely on the density of population. Field mice commonly breed in central New York from mid-March until mid-November. Except during the third or fourth year of the cycle, the mouse numbers usually have not reached excessive proportions and the mice do not customarily breed during the winter months (December to February). In the year of greatest mouse abundance, cold weather curtails winter breeding greatly, yet a fair proportion of the animals continue to produce young throughout the winter. A considerable decrease in the litter size and frequency of breeding during the winter is, however, apparent. There was no indication of cessation of breeding during the winter of 1935–36 as was evident in the previous two winters (fig. 2). Following a period of reduced mouse populations in the spring and summer of 1936, it became evident that a smaller share than usual of the surviving mice were breeding.

FACTORS RESPONSIBLE FOR DECREASE IN NUMBERS

Abiotic factors, such as climatic conditions, might conceivably have a limiting effect upon animal populations. Biotic factors, such as abundance of predators or parasites and disease, might likewise account for an appreciable toll.

CLIMATIC CONDITIONS

Climatic conditions apparently exerted little influence in minimizing a steady increase of the murine population from the winter of 1932 until 1935. Snow acts as protection for mice, both by discouraging predators and by excluding frost from the ground. Mice were extraordinarily abundant in central New York during the winter of 1931–32, yet in the area under investigation there were but 6 days during December, January, and February in which more than 2 inches of snow remained on the ground. After a sharp decrease in numbers, mice began to increase during the winter of 1932–33, yet on only 15 days of the entire winter did snow remain on the ground to a depth of 2 inches.

Similar conditions prevailed during the winters of 1933–34 and 1934–35. The mice showed greatest increase in the fall and early winter of 1935 and continued abundant until late spring of 1936. Prolonged periods of deep snow during the winter undoubtedly helped the mice to increase. On the other hand, prolonged dry periods limit the increase. Reports from the Midwest had indicated that the peaks in mouse population occurred synchronously with those in the East during 1923–24, 1927–28, and 1931–32. While the voles were again abundant in Michigan, Indiana, Illinois, and Wisconsin during the winter of 1935–36, they were still abundant in this area during the summer of 1936. The prolonged drought at this time may have delayed appearance of the peak.

Orchardists frequently attribute mouse abundance and consequent damage to prolonged periods of heavy snowfall. In central New York during the winter of 1930–31 snow remained on the ground from mid-December until mid-March, yet mice were not abundant nor was there any considerable damage. A similar situation prevailed during the winter of 1922–23, yet mice were not particularly abundant and little damage resulted. A combination of prolonged periods of deep snow synchronous with peaks in mouse population usually cause severe damage.

Unlike the emigrations of lemmings and gray squirrels, which appear to indicate peaks in the populations of these animals, there is no indication of mass movements of microtines. When the high of a cycle has been achieved, there usually is no territory for the animals to preempt, for all suitable cover is well populated with their kin.

PREDATORS

Carnivorous enemies, such as dogs, cats, foxes, weasels, skunks, hawks, and owls, while undoubtedly preventing local outbreaks upon occasion, can do little to check high populations which are a natural phenomena of the lives of cyclic rodents. The rodent's power of reproduction is so great, that once their numbers have passed a crucial stage, the slow-breeding predators cannot control them. If the outbreaks were extremely local, predators might flock to the area and successfully cope with the situation. Such peaks, in the East, usually occur over an area extensive enough to prevent any concentration of predators at a given point. In the western United States, outbreaks of rodents have usually been of a relatively local nature, and predators then swarm to the locality, taking colossal toll of the mice. Inasmuch as the increase leading to a maxima usually takes

takes place within a single breeding season, or two at the most, there is little chance for carnivores to successfully combat these pests.

DISEASE AND PARASITES

All available evidence indicates that disease is the control factor that terminates these mass increases of rodents. Piper (*6*) has recorded many dead and dying voles after the peak of the Nevada mouse plague of 1907–8. While the mice were ostensibly killed by disease, all attempts to isolate a specific bacterial disease met with failure.

The 1926–27 outbreak in Kern County, Calif., consisted chiefly of the house mice (*Mus musculus*), although meadow mice (*Microtus californicus*) were estimated at 4,000 per acre. According to Selle (*10*) 200 of these mice, brought into the laboratory, were found to be suffering from symptoms of an infection which caused them to snuffle and their eyes to secrete a yellowish serous fluid. Selle states that more than half the mice were lost in the first month of captivity. The epizootic was likewise studied by Wayson (*13*) who performed necropsies on many of the morbid microtines, and was able to isolate the causative bacillus of mouse septicemia (*Bacillus murisepticus*) or swine erysipelas (*B. rhusiopathiae*) both of which are considered identical by Preisz (*9*).

Recently Findlay and Middleton (*3*), during a period of mortality among wild voles (*Microtus agrestis*) found the only apparent cause of death has been the presence of cysts of a toxoplasm (*Toxoplasma microti*) in the brains. Elton, Davis, and Findlay (*2*) record a severe epidemic which destroyed many voles, the causative agent being a protozoan (*Toxoplasma*) infection of the brain.

Where great masses of mice assemble following a rapid increase in numbers, the spread of contagious disease is spectacular. A large proportion is quickly destroyed, and few escape the plague. In the eastern United States, where the rodents pass through less spectacular increases, the hordes are more evenly spaced over large areas of suitable habitat and accordingly spread of disease is limited.

That disease was the paramount factor in reducing the 1936 spring population of mice cannot be denied. Edwin H. Buerman, a professional bridge grafter of Williamson, N. Y., grafted trees in western New York daily during June 1936. He informed the writer that while mice were very abundant during the previous fall and winter, few live ones were observed during June. Dead mice, adults and young, were found in their nests on several occasions. Several students of the writer likewise found dead mice in nests during early spring. LeRoy Garnsey of Seneca Falls, N. Y., was in the field constantly during the spring and summer of 1936. He found large numbers of dead mice on his farm, which, upon examination showed no marks or injury of any nature.

Voles taken in late March exhibited symptoms similar to those described by Findlay and Middleton (*3*). The mice became sluggish, the fur stood on end, becoming damp and slightly oily, and lethargy was pronounced. After incipient drowsiness, a characteristic spasmodic twitching of the neck and shoulders was manifest, the animal soon falling on its side. Watery discharges from the vent and gasping accompanied this final stage, the animals thrusting their hind legs

straight backward. Convulsive activity soon resulted in death. Eleven captives exhibited such clinical symptoms with resultant fatality.

Laboratory analysis of two mice exhibiting convulsive behavior was made by Dr. Alexander Zeissig of the New York Veterinary College. His observations are recorded below.

Gross examination.—All of the internal organs appear normal except the liver which in both specimens contained a large cyst near the periphery of the organ. The cysts measured 2 by 1.5 cm and the shape was that of an almond. On opening the cyst what appeared to be the cystic form of a tapeworm was found.

Cultural examination.—About 0.3 cc of the heart blood was removed under aseptic precautions with a Pasteur pipette and transferred to an agar slant. After several days incubation the medium remained sterile.

Microscopical examination.—A smear was made from the heart blood and stained with Wright's stain. No blood parasites were observed.

Unfortunately the small number examined is not indicative nor do the observations preclude the possibility of the presence of a filterable virus.

Blood smears were stained and studied repeatedly during the spring and summer of 1936, but no indication of blood parasites was found.

Inasmuch as the stricken mice exhibited symptoms which suggested cerebral irritations, brains were removed from comatose mice, sectioned, stained, and a thorough study was made for toxoplasms or other contributory disease organisms. None was found.

At the peak of the cycle, and during its decline, bladder worms were found in the liver of approximately one-fourth of the mice. These were determined as the cysticercus, or bladder worm stage, of *Taenia taenieaformis* Wolffhuegel by E. W. Price, Bureau of Animal Industry, United States Department of Agriculture.

While microtines always support a population of external parasites, ectoparasites were uncommonly abundant during late 1935 and early 1936. Aside from their mechanical irritation and consumption of blood, certain arthropod species are responsible for the transmission of destructive infectious diseases. Ectoparasites were determined by H. E. Ewing, Bureau of Entomology and Plant Quarantine, United States Department of Agriculture.

The most abundant parasite, a louse (*Hoplopleura a. acanthopus* (Burm.) was, during this period, much in evidence. More than a thousand were taken from one mouse; it was not uncommon to recover 300 or 400 from single animals during March and April 1936. Mites were likewise abundant, especially *Laelaps microti* (Ewing) and *Atricholaelaps glasgowi* (Ewing). *Laelaps* frequently numbered in excess of 200 per mouse. Two fleas, *Orchopeas leucopus* (Bak.) and *Ctenophthalmus pseudagyotes* Bak., were not uncommon, occasionally six fleas being recovered from one mouse. Fleas and lice persisted on the mice for 20 hours after death of the rodent.

FORECASTING MOUSE YEARS

It is highly desirable to know the expectant high in a mouse cycle, for control measures can be inaugurated before severe infestations occur and the resultant loss thus minimized. It has been shown that the highs in mouse populations occur periodically, usually at intervals of 4 years. Past high populations have occurred in the winters of 1919–20, 1923–24, 1927–28, 1931–32, and 1935–36. Extended records

are not available prior to this period, but scattered reports indicate a regular periodicity of the cycle since 1863.

Assuming there will be no deviation from this frequency, we may look for the next high in 1939–40 and every fourth year thereafter. Eternal vigilance and constant warfare should not be relaxed, for local conditions often permit exaggerated populations to appear before the anticipated climax to the cycle. Based on observations outlined in this paper, it was possible to forecast high populations of mice 18 months before their appearance, while the mouse population was far from numerous. Following extensive warnings and suggested field practices 1½ years prior to the outbreak, orchardists were able to safeguard their trees in part from the most severe mouse infestation New York has ever experienced.

SUMMARY

Field mice (*Microtus pennsylvanicus*) exhibit variable populations from year to year. A 4-year cycle has been established for northeastern United States. From a low of 15 to 40 mice per acre after the periodic decline, populations build up to from 60 to 250 per acre in 3 or 4 years.

Increased population is fostered by three reproductive factors: (1) An acceleration of the breeding rate; (2) an increased number of young per litter; and (3) the lengthening of the reproductive season, which allows for greater numbers of litters per year.

Causes responsible for a decrease in numbers of mice may be abiotic, such as climatic influences, or biotic, such as diseases, predators, etc. It appears that murine epizootics occurring when mice have reached the peak of their abundance, are the primary causative agent reducing mouse populations. Plagues of mice are often accompanied by disease of an epidemic nature among these animals.

Forecasting the years of mouse abundance is important, for control methods may be inaugurated before the expected period of peak population, and the extent of the damage minimized. Past periods of great mouse abundance in New York were the winters of 1919–20, 1923–24, 1927–28, 1931–32, and 1935–36. Peaks of future cycles may thus be expected in the winters of 1939–40, 1943–44, and so on. Increase in mouse populations occur rapidly, so that optimum densities may be reached in 2 or 3 years following a low. Thus perpetual vigilance of the agriculturists and especially the orchardists is necessary at all times.

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CHANGES IN WEIGHT AND NITROGEN CONTENT OF ADULT WORKER BEES ON A PROTEIN-FREE DIET [1]

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INTRODUCTION

The effects of starvation on insects were studied by several workers. Slowtzoff (*14, 15, 16, 17*)[3] and Heller (*5*) obtained data on losses in weight, water, dry matter, fats, and proteins in various species of starved insects. However, their determinations were based on the analyses of the whole bodies of the specimens investigated. It is very probable that the intestinal content of the insects may to a greater or lesser degree have obscured the real changes that had taken place. Removal of the digestive tract before analysis would give a clearer picture of what is actually happening to the animal body during starvation.

There is a period in the life of the bee that resembles a partial starvation. With the arrival of cold weather, a colony of bees forms a cluster and passes the winter living to a great extent on a carbohydrate diet. This is especially true when bees do not have stores of pollen in the hive. Under such circumstances they undoubtedly do not have any source of proteins to restore the losses from nitrogen catabolism. By analyzing various parts of the bodies of such bees, the changes that occur during protein starvation may be determined. Parhon (*8*) made a very comprehensive study of the changes taking place in the bodies of bees during an entire year. She could not, however, detect any appreciable variation in the nitrogen content of bees during that time. Whole bees were used in these determinations.

Preliminary analyses made by the writer indicated that considerable changes in the nitrogen content occur in bees on a pure carbohydrate diet. Therefore it was decided to undertake a more elaborate study of such changes in 1932 and 1933.

METHOD

For 3 days emerging bees were brushed into a small hive onto a comb containing honey and pollen. This hive was kept in an isolated compartment of a greenhouse. A fertile queen was added to the colony. The bees were allowed to develop and to start the rearing of brood. As soon as the first sealed cell was noticed, the bees were transferred to a new compartment and hived on a newly built comb containing neither honey nor pollen. Sugar solution and water were then offered in quantity throughout the experiment. The bees started to rear brood anew but soon ceased their nursing activity. The comb with the sealed brood was removed from the hive and the bees were again transferred to another hive containing an empty new comb. There

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[3] Reference is made by number (italic) to Literature Cited, p. 795.

was no brood-rearing activity after that time. Weekly changes in the weight and nitrogen content of the bees were determined throughout the duration of the experiment, using the technique already described (*2*). The nitrogen content of the dry bees was ascertained. The changes were followed for 189 days on the protein-free diet. Bees in the last sample were 236 days old.

RESULTS AND DISCUSSION

The results of the experiment are given in tables 1 to 3. The numbers in the first table represent averages from three weekly determinations (about 60 bees).

TABLE 1.—*Fresh and dry weight and nitrogen content of whole bees, of various parts of them, and of their alimentary tracts and contents, after different periods on a nitrogen-free diet* [1]

FRESH WEIGHT

Age of bees (days)	Duration of diet	Heads	Abdomens	Thoraces	Whole bees	Bees with alimentary tracts removed	Alimentary tracts and contents
	Days	*milligrams*	*milligrams*	*milligrams*	*milligrams*	*milligrams*	*milligrams*
47	0	12.2	22.3	39.7	125.5	74.2	51.3
68	21	11.9	20.0	39.1	131.8	71.0	60.8
89	42	12.3	12.0	40.7	140.2	65.0	75.2
110	63	10.9	12.0	39.3	127.8	62.2	65.6
131	84	12.1	14.2	39.7	123.8	66.0	57.8
152	105	11.1	10.9	38.9	116.8	60.9	55.9
194	147	10.7	11.0	39.4	120.6	61.1	59.5
215	168	10.0	11.6	38.8	108.3	60.4	47.9
236	189	10.0	12.1	39.1	108.5	61.2	47.3

DRY WEIGHT

47	0	3.7	12.0	13.4	41.3	29.1	12.2
68	21	4.1	8.0	14.0	42.8	26.1	16.7
89	42	3.5	4.1	13.7	44.3	21.3	23.0
110	63	3.5	4.5	13.5	42.5	21.5	21.0
131	84	3.8	5.5	13.1	40.3	22.4	17.9
152	105	3.4	3.8	13.0	40.2	20.2	20.0
194	147	3.5	3.3	13.4	38.5	20.2	18.3
215	168	3.1	2.8	12.5	32.4	18.4	14.0
236	189	3.1	3.3	12.9	33.7	19.3	14.4

NITROGEN CONTENT [2]

47	0	0.41	0.47	1.69	3.30	2.57	0.73
68	21	.37	.46	1.62	3.20	2.45	.75
89	42	.34	.37	1.64	3.03	2.35	.68
110	63	.33	.34	1.62	2.92	2.29	.63
131	84	.35	.34	1.58	2.95	2.27	.68
152	105	.32	.30	1.52	2.72	2.14	.58
194	147	.29	.30	1.56	2.86	2.15	.71
215	168	.31	.31	1.55	2.51	2.17	.34
236	189	.26	.26	1.48	2.57	2.00	.57

[1] Based on averages of 3 weekly determinations. [2] Based on dry weight of parts.

TABLE 2.—*Final percentage changes in values for fresh and dry weight and nitrogen content of whole bees, of various parts of them, and of their alimentary tracts and contents, after different periods on a nitrogen-free diet*

Value	Age of bees	Duration of diet	Heads	Abdomens	Thoraces	Whole bees	Bees with alimentary tracts removed	Alimentary tracts and contents
	Days	*Days*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Fresh weight	236	189	−18.0	−45.7	−1.5	−13.5	−17.5	−7.8
Dry weight	236	189	−16.2	−72.5	−3.7	−18.4	−33.7	+18.0
Nitrogen	236	189	−36.6	−44.7	−12.4	−22.1	−22.2	−21.9

TABLE 3.—*Dry matter, and nitrogen in the fresh and dry matter, of whole bees, of various parts of them, and of their alimentary tracts and contents, after different periods on a nitrogen-free diet*

Parts of bee body	Dry matter			Nitrogen in fresh matter			Nitrogen in dry matter		
	Mean	Standard deviation	Coefficient of variation	Mean	Standard deviation	Coefficient of variation	Mean	Standard deviation	Coefficient of variation
	Pct.	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*
Heads	31.1±0.336	1.497	4.8	3.0±0.049	0.218	7.4	9.4±0.180	0.800	8.5
Abdomens	35.6±1.838	8.176	23.0	2.5± .084	.374	15.0	7.6± .442	1.967	25.9
Thoraces	33.7± .214	.954	2.0	4.0± .031	.137	3.4	11.9± .081	.360	3.0
Whole bees	32.3± .274	1.217	3.8	2.3± .031	.139	6.0	7.3± .387	.410	5.6
Bees with alimentary tracts removed	34.0± .550	2.445	7.2	3.5± .026	.115	3.3	10.4± .187	.831	8.0
Alimentary tracts and contents	30.1± .701	3.118	10.4	1.1± .944	.196	17.8	3.7± .236	1.050	28.4

When an animal does not receive nitrogenous food, it derives its nitrogen mainly from its muscular tissues. According to Roche (*9, 11, 12, 13*), rats derive such nitrogen, not from special proteinaceous reserves, but from the catabolism of muscular proteins. In bees, protein can be stored, presumably in the fat body (*18*). However, other parts of the bee body apparently contribute their share of nitrogen in case of protein starvation.

Examination of table 1 shows that there was a substantial decrease both in weight and the nitrogen content of all parts of the bodies of the experimental bees. These results differ somewhat from those obtained by other workers. Keller-Kitzinger (*6*) kept bees for 3 weeks on a pure carbohydrate diet and did not find any appreciable changes in the nitrogen content of their bodies. She concluded that bees cannot use proteins in catabolic processes. The fact that there was no appreciable change in the nitrogen content of whole bees fed for 3 weeks on a protein-free diet was confirmed by the writer (loss of 4.7 percent), but the conclusion of the author mentioned should be modified since bees apparently do catabolize proteins, a fact that is evident when they are kept on a protein-free diet for a longer time.

From table 2 it is evident that the greatest losses in the weight and in the nitrogen content of the bees were in the abdomen. Since the alimentary tracts were removed before the determinations were made, the losses cannot be attributed to the changes in the fecal content of the recta, but must be changed to processes that took place in the abdominal tissues. This still further confirms previous findings (*1, 3, 4*) that the composition of the abdomens of bees is influenced most by their diet, or by the diet of the larvae. The final increase in the dry weight of the digestive tracts was apparently due to a greater fecal content of the recta of the bees in the last sample and cannot be considered as significant.

It is interesting to note that Slowtzoff (*14, 15, 16, 17*) and Heller (*5*) found an increase in the percentage of dry matter of the starved insects used in their experiments. This phenomenon can be explained by the fact that, in the experiments of the latter investigators, the insects were deprived of all food, hence the increase in the percentage of dry weight should be attributed to the loss of water which they could

not restore. The loss of water was even the main cause of death in some species investigated (bumblebees, dragonflies).

In the writer's experiment there was a final decrease in the percentage of dry matter, as well as in the percentage of nitrogen in the fresh and dry weights of the experimental bees. The exception was a slight increase in the percentage of the dry matter of the heads (from 30.3 to 31) and intestines (23.8 to 30.4), and a considerable increase in the percentage of nitrogen in the dry matter of the abdomens (from 3.9 to 7.9). There was no change in the percentage of nitrogen in the fresh weight of the abdomens.

The increase in the percentage of nitrogen in the dry matter of the abdomen is rather significant. If we compare it with the largest decrease in the total nitrogen and in the dry matter of the abdomens, we have to assume either that most of the stores of glycogen and fat were depleted, leaving a part of the proteins intact, or that the products of nitrogen catabolism were deposited in some parts of the abdomen, as the stored nitrogen was depleted. Since the organism was in need of nitrogen and there was a storage place for that element in the abdomen it is unlikely that any of the usable nitrogen would be left in storage.

On the other hand, with the stores of the fat body depleted the only nitrogenous substance, is the chitinous cover, which comprises the greatest part of the abdomen. The nitrogen content of chitin is about 8 percent (*19*), which closely corresponds to the final percentage of nitrogen in the abdomens (table 3).

Another possible cause of this increase is the deposition of the metabolic waste in the oenocytes of the fat body, an assumption which was suggested by Koschevnikov (*7*). In an emerging bee the oenocytes are clear, but with age, greenish-brown granules are deposited in them. An old bee has oenocytes packed with such granules. If we assume that they are products of catabolic processes, transitionally deposited in the abdomen, then the large variation in the percentage of nitrogen in the dry matter could be explained by the variation in the uric acid content of oenocytes, and possibly of some other organs or structures in the abdomen.

Slowtzoff reported an increase in the percentage of nitrogen in the fresh matter of starved insects. There was a decrease in the percentage of nitrogen in the dry matter. Heller found an increase in both cases. The increase in the percentage of nitrogen in the fresh matter can be explained mainly by the loss of water from the bodies of starved animals. The increase in the percentage of nitrogen in the dry weight was undoubtedly due to the depletion of stores of fat and glycogen, plus the possibility that the products of protein catabolism were retained in the bodies of the experimental insects. Roche (*10*) also found an increase in the percentage of nitrogen in the fresh weight of fasting rats.

The greatest variation was in the percentage of dry matter and of nitrogen in the abdomens of the experimental bees (table 3). This is not surprising, because abdomens are influenced the most by any change in the diet, and they may be considered as transient stations of all the waste products of protein catabolism. The smallest variation was in the thoraces of bees. Thoraces, composed for the most part of muscles and chitin, are not likely to be profoundly influenced by the intermediary deposits of the products of protein catabolism.

Large variation in the composition of the intestinal contents is significant and should be taken into account when determinations are made on whole insects. These variations may considerably obscure values for the actual composition of the bodies of insects under investigation.

SUMMARY

An experiment has been described in which bees of a known age were fed a pure carbohydrate diet for a period of 189 days. The bees in the last sample were 236 days old. Weekly changes in the fresh and dry weight, and in the nitrogen content of heads, abdomens, thoraces, and whole bees were ascertained.

There was a substantial decrease both in weight and in nitrogen content of all parts of the bodies of the experimental bees, the greatest change taking place in the abdomens.

A final decrease in the percentage of dry matter and of nitrogen in the fresh and dry weights occurred in the experimental bees. A slight increase in the dry matter of the heads and intestines, and a considerable increase in the percentage of nitrogen in the dry matter of abdomens were exceptions. The significance of the latter findings is discussed.

The greatest variation was in the percentage of dry weight and of nitrogen in the abdomens of the experimental bees. The smallest variation was in the thoraces.

The necessity of removing the intestines before analyzing insects is emphasized.

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